MICROBIOLOGICAL REVIEWS, June 1978, p. 357-384
0146-0749/78/0042-0357$02.00/0
Copyright © 1978 American Society for Microbiology
Vol. 42, No. 2
Printed in U.S.A.

Genetics of *Rhodospirillaceae*

VENETIA A. SAUNDERS†

Department of Biochemistry, University of Liverpool, Liverpool L69 3BX, United Kingdom

INTRODUCTION

Photosynthetic bacteria have been effectively used for many years as model systems for investigating photosynthesis and related metabolic phenomena. Although this has led to a considerable accumulation of biochemical and biophysical data concerning the mechanics of bacterial photosynthesis (for example, 26, 27, 58, 73, 101, 173, 174), there has, until recently, been a conspicuous lack of complementary genetic information. A profound analysis of the genetics of the photosynthetic bacteria would certainly enhance their present status as research tools. This would, in turn, afford unique opportunities for exploring the development and function of energy-conserving systems.

One of the primary aims in studying the molecular biology of photosynthetic bacteria is to determine the nature, arrangement, and activity of those genes specifying the photosynthetic apparatus. Accordingly, this paper considers progess made towards this goal and outlines potential avenues of inquiry. Some emphasis will be laid on physiological processes of the photosynthetic bacteria which are amenable to investigation via the construction and subsequent analysis of specific mutants. Indeed, this kind of approach has contributed substantially to the current volume of literature regarding these photosynthetic organisms.

The photosynthetic procaryotes presently comprise the cyanobacteria (blue-green algae), the prochlorophyta, and the green and purple bacteria (179). (For the purposes of this review, the photosynthetic bacteria refer to the green and purple bacteria.) Four families are recognized within the green and purple groups: the *Chlorobiaceae* (green and brown sulfur bacteria), the *Chloroflexaceae* (filamentous gliding green bacteria), the *Chromatiaceae* (purple sulfur bacteria), and the *Rhodospirillaceae* (purple nonsulfur bacteria) (179, 180). This review of necessity focuses on the latter family, reflecting the limits of existing knowledge. An attempt is also made to integrate pertinent aspects of the cyanobacteria in line with reports of a close affinity between these and other procaryotes (for example, 36, 43, 53, 59, 227, 229, 253).

For more extensive coverage of the genetics of

† Present address: Department of Biology, Liverpool Polytechnic, Liverpool L3 3AF, United Kingdom.

the cyanobacteria refer to recent reviews of Wolk (273) and Delaney et al. (43).

PHYSIOLOGICAL ASPECTS

Photosynthetic bacteria are unique amongst phototrophs in respect of the anaerobic nature of bacterial photosynthesis. No oxygen is evolved in the process, and oxidizable substrates other than water serve as electron donors (70, 177, 224, 259). On the other hand, the cyanobacteria typically exhibit oxygenic photosynthesis in a process comparable to that operative in photosynthetic eucaryotes (65, 112). Most photosynthetic bacteria and certain cyanobacteria are capable of utilizing atmospheric nitrogen as their sole nitrogen source for photosynthetic growth (65, 69, 72, 103, 170, 232-234, 273).

Typical representatives of the *Rhodospirillaceae* (purple nonsulfur photosynthetic bacteria) are facultative anaerobes possessing the adaptive capacity to grow anaerobically in the light (photosynthetically) and aerobically in darkness (by oxidative phosphorylation). Certain members of this family are also capable of growing anaerobically in the dark (251, 277). *Rhodopseudomonas sphaeroides*,, *Rhodopseudomonas palustris*, and *Rhodospirillum rubrum* can ferment pyruvate under strictly anaerobic conditions in darkness (251). However, growth of *Rhodopseudomonas capsulata* under such conditions necessitates addition of dimethyl sulfoxide to the growth medium (277). By virtue of their metabolic versatility, these photosynthetic bacteria are particularly well suited to the study of processes involved in the formation and differentiation of energy-conserving membranes. Moreover, mutant strains can be readily isolated that are either photosynthetically or aerobically incompetent, but capable of growing in the alternative energy conversion mode. Such mutants have been effectively exploited in examining the electron transport systems of these organisms as discussed below (see Towards Elucidation of Electron Transfer Systems). The general physiologies of the photosynthetic bacteria and the cyanobacteria have been detailed elsewhere (for example, 23, 60, 71, 73, 106, 110, 170, 177, 224, 228, 258, 273).

EVOLUTIONARY CONSIDERATIONS

There is considerable speculation about the evolutionary significance of the photosynthetic procaryotes (18, 21, 35, 49, 168, 185, 197, 225, 226, 244). On the one hand, ancestors of the photosynthetic bacteria are presumed to be amongst the earliest of organisms utilizing radiant energy in an anaerobic environment (168, 197). On the other, ancestors of cyanobacteria were supposedly responsible for early biological oxygen production and hence for the dramatic evolutionary consequences stemming from this transition in the gaseous environment (18, 30, 65, 168). Cyanobacteria have for some time been cited as likely candidates for endosymbiotic precedents to photosynthetic plastids of certain eucaryotic cells (136, 146, 226, 237, 244). More recently, it has been suggested that ancestors of some contemporary respiring bacteria may have evolved from some purple nonsulfur photosynthetic bacteria by atrophy of their photosynthetic capacity. Likewise, certain of the gliding bacteria may have derived from cyanobacteria (49).

Data concerning the structure and sequence of electron transfer proteins which have been amassed in recent years (for example, 5-8, 49, 214, 240-242, 245, 255, 260, 275) may provide some clues to evolutionary connections between procaryotes and eucaryotes. Close structural and sequence similarities are apparent for cytochrome c_2 from purple nonsulfur bacteria (8, 56, 198), cytochrome c_{550} from *Paracoccus denitrificans* (247-249), and mitochondrial cytochrome *c* (41, 47, 48). These findings, together with the similarities in respiratory electron transfer properties of *P. denitrificans*, the purple nonsulfur bacterium *R. sphaeroides*, and the mitochondrion (58, 99, 204), encouraged speculation about the evolution of bacterial energy metabolism. Dickerson and colleagues (49) have suggested that "the point of divergence between photosynthesis and respiration occurred in the ancestors of purple nonsulfur photosynthetic bacteria." However, phylogenetic relationships between organisms may well have been blurred via the agency of genetic exchange (cf. reference 6); thus, interpretations of evolutionary occurrences based on such molecular methodology may prove to be oversimplifications of actual events.

Comparison of amino acid sequence similarities between *f*-type cytochromes from certain cyanobacteria and eucaryotic algae indicate a closer sequence correlation between the cytochrome *f* of the cyanobacteria and that of the red algae than with that of any other algae (5, 7). Aitken (5) points out that, although genetic transfer may have occurred, obscuring the interrelatedness of such photosynthetic proteins, protein sequence studies have produced much information in keeping with the hypothesis of a common origin of oxygenic photosynthesis in procaryotes and eucaryotes. Indeed, patterns of homologies from ribosomal ribonucleic acid (RNA) sequence studies with cyanobacteria and chloroplasts (16, 17, 52, 175) lend credence to this notion.

Recently, certain "procaryotic green algae" have been observed and studied which possess a unique combination of characteristics, some typically procaryotic and others eucaryotic (127). Significantly, these organisms contain both chlorophyll *a* and chlorophyll *b* and perform oxygen-evolving photosynthesis. Whether these algae or relatives are progenitors of green plant chloroplasts remains open to question.

STUDIES WITH MUTANTS

Mutant strains of various microorganisms have proven invaluable in the elucidation of a number of metabolic pathways. Of particular relevance here are those mutants of photosynthetic procaryotes that facilitate studies on electron transfer processes, nitrogen fixation, pigment biosynthesis, membrane development and differentiation, and related biological phenomena.

Typical mutants of the *Rhodospirillaceae* are obtained by ultraviolet irradiation or *N*-methyl-*N'*-nitro-*N*-nitrosoguanidine mutagenesis essentially by the method of Adelberg et al. (3), with or without subsequent penicillin screening (124). Less frequently, mutants have been isolated after spontaneous mutation. Mutations in the cyanobacteria are commonly induced with nitrosamines. Fairly extensive surveys of the mutants of cyanobacteria have recently appeared (43, 254).

This section is confined to a description of mutants of the *Rhodospirillaceae*. These mutants not only represent valuable research tools in biochemical investigations but also provide a bank of genetically marked strains convenient for gene transfer studies.

Survey of Mutants of the *Rhodospirillaceae*

Various classes of mutants of the *Rhodospirillaceae* have been reported, most commonly for *R. sphaeroides*, *R. capsulata*, and *R. rubrum*.

Resistant mutants. A range of antibiotic-resistant mutants has been obtained, including strains resistant to rifampin, streptomycin, nalidixic acid, and kanamycin (142, 153, 206, 217, 222, 262, 276, 277; V. A. Saunders, Ph.D. thesis, University of Bristol, Bristol, U.K.). Mutant strains of *R. capsulata* resistant to arsenate have also been isolated (for example, 281). One such mutant, strain Z-1, exhibits enhanced rates of photophosphorylation. After prolonged culture in the presence of arsenate, cells have elevated contents of cytochromes, reaction center bacteriochlorophyll, and photophosphorylation coupling factor (129, 281). This class of mutants should prove useful for analyzing mechanisms of energy conservation in photosynthetic bacteria.

Auxotrophs. Mutants requiring specific amino acids have been described (for example, 13, 14, 78, 126, 217, 222, 276, 277). Adenine-requiring (unpublished data) and uracil-requiring (125) mutants of *R. sphaeroides* have been prepared and used in the radiolabeling of deoxyribonucleic acid (DNA) and RNA, respectively. Certain glycerol-requiring strains of *R. capsulata* have recently been isolated and characterized (108). A series of mutants of *R. capsulata* have been obtained that lack the capacity to fix nitrogen (Nif^-) (264) presumably because of the absence of nitrogenase activity or because of defects associated with the synthesis or metabolism of glutamine or glutamate (262, 264).

Pigment mutants. The *Rhodospirillaceae* synthesize colored carotenoids belonging to the "spirilloxanthin series" (98). In *R. capsulata* and *R. sphaeroides*, spheroidene and hydroxyspheroidene predominate under anaerobic conditions in the light. On the other hand, *R. rubrum* synthesizes mainly spirilloxanthin. Various mutants with altered carotenoid complement are known. Classical "blue-green" mutants, lacking colored carotenoids and accumulating phytoene, have been described for *R. sphaeroides* (for example, 29, 80, 81, 216, 218, 219), *R. capsulata* (for example, 55, 267, 276), and *R. rubrum* (for example: 39; R. K. Clayton, cited in references 95 and 113). "Green" mutants, presumably blocked at the neurosporene or chloroxanthin stages of carotenoid biosynthesis, have been obtained for *R. sphaeroides* (for example: 37, 38, 80, 81, 145, 203; Saunders, Ph.D. thesis) and *R. capsulata* (267, 276). Yen and Marrs (276) recently described "yellow" mutants of *R. capsulata* that apparently were phenotypically indistinguishable from the so-called brown mutants of *R. sphaeroides* isolated by Griffiths and Stanier (81). Further "brown" mutants, phenotypically distinct from those of Griffiths and Stanier (81), have also been characterized (210). Furthermore, certain mutants of *R. sphaeroides* have been isolated that combine the traits of carotenoid deficiency and a high catalase activity (29).

There is a spectrum of mutants with blocks at specific stages in bacteriochlorophyll biosynthesis (Table 1). The propensity of such mutants for accumulating various tetrapyrrole pigments, presumably bacteriochlorophyll precursors, has contributed significantly to the elucidation of reactions involved in bacteriochlorophyll biosynthesis as outlined in the following section. The inability of "albino" mutants to form carotenoid and bacteriochlorophyll is possibly a manifestation of loss or dysfunction of a genetic

TABLE 1. *Typical mutants of photosynthetic bacteria with lesions affecting bacteriochlorophyll biosynthesis*

Species	Mutant strain	Remarks	Reference
R. sphaeroides	H-4, H-5	Lack δ-aminolevulinate synthase activity, require aminolevulinate for growth; H-5 normalized by aminolevulinate	121
	6-6	Excretes porphobilinogen, no magnesium tetrapyrroles formed	120
	2-33 (Met^-)	Excretes coproporphyrin, methionine pathway blocked at homocysteine methylation level	117
	M-17 (Met^-)	Excretes coproporphyrin, methionine pathway blocked at stage before cysteine synthesis	126
	2-73, V-3	Excretes magnesium divinylpheoporphyrin a_5	116, Saunders, Ph.D. thesis
	8-32	Excretes magnesium divinylpheoporphyrin a_5, bacteriochlorophyllide, and heme	188
	"Tan"	Magnesium divinylpheoporphyrin a_5 accumulated by cells	228
	"Griffiths mutants"	Magnesium divinylpheoporphyrin a_5 (and, probably, later intermediates) accumulated by cells	79
	2-21	Excretes 2-devinyl-2-hydroxyethylchlorophyllide a	116
	8-29	Excretes 2-devinyl-2-hydroxyethylchlorophyllide a and some pheophorbide a	188
	8-47, 8-53	Excrete 2-desacetyl-2-hydroxyethylbacteriochlorophyllide and 2-devinyl-2-hydroxyethylchlorophyllide a	188
	8-17	Excretes bacteriochlorophyllide	188
	8-13	Accumulates heme, no magnesium tetrapyrroles formed	120
	L-57, 3-1, V-2	"Albino" mutants, neither bacteriochlorophyll nor precursors formed, also fail to make carotenoids	120, 204
	"Griffiths mutants"	"Albino" strains, neither bacteriochlorophyll nor carotenoids formed	81
	L-57 R, TA-R, DW-R	Cells accumulate bacteriochlorophyll aerobically in darkness	123
	8	Excretes 2-desacetyl-2-vinylbacteriopheophorbide	184

TABLE 1—*Continued*

Species	Mutant strain	Remarks	Reference
	O_1	Excretes pigments with absorbance maximum below 660 nm	102
R. rubrum	F3, F4, F6	Excrete magnesium divinylpheoporphyrin a_5 monomethylester	165
	F5, F8, F9	Excrete 2-devinyl-2-hydroxyethylpheophorbide a, some pheophorbide a	163, 165
	F12	Excretes 2-devinyl-2-hydroxyethylpheophorbide a, some pheophorbide a and bacteriochlorophyll	165
R. capsulata	A1a (Pho^-)	Excretes phytylated (fully esterified) magnesium-2-vinylpheoporphyrin a_5 as protein complex	55
	Y80, Y491	Accumulates precursor with absorbance maximum at 630 to 635 nm (presumably magnesium 2,4-divinylpheoporphyrin a_5)	276, 277
	SB21, Y34, Y62, Y92, Y121, Y122, Y165, Y167, Y451	Accumulate precursor with absorbance maximum 665–670 nm	276, 277
	W1, Y89	Incapable of synthesizing bacteriochlorophyll and carotenoids	263, 277
	HH 910, HH 911	Accumulate precursor with absorbance maximum at 730 nm	277
R. palustris	Green 1, 2, 3, Yellow	Magnesium divinylpheoporphyrin a_5 and a phytylated form extracted from cells	63, 111, 223, 252

element governing synthesis of the entire photopigment system. Alternatively, synthesis of the photosynthetic membrane components may be dependent on the assembly process; thus, if any one of the structural components was absent, synthesis of the entire system would be switched off. A photosynthetically incompetent strain of *R. rubrum* has been isolated which produces a "pheophytin-protein-carbohydrate" complex. Some nonfunctional bacteriochlorophyll is also formed. Failure of the pigment complex to associate with the membrane may reflect alteration or absence of requisite components for its incorporation (207). In addition, a mutant of *R. sphaeroides* has recently been described which accumulates 4-vinyl protochlorophyllide, presumably because of defective synthesis of membrane components required for incorporation of bacteriochlorophyllide into the intracytoplasmic membrane system (183).

Electron transfer mutants. Mutants with specific defects in the respiratory or photosynthetic electron transfer system have been described (for example, 44, 45, 115, 138, 139, 141, 272). The biochemical lesions affecting some of them will be considered below (see Towards Elucidation of Electron Transport Systems). Certain strains of *R. sphaeroides* (216, 218, 239) and *R. capsulata* (277) lack functional reaction center bacteriochlorophyll (P870), whereas they synthesize the light-harvesting (bulk) bacteriochlorophyll. Accordingly, such mutants do not manifest those activities associated with the primary photochemistry of photosynthetic cells (211, 218, 220). Mutants of *R. rubrum* have also been reported with properties characteristic of strains with defective reaction centers (44, 181).

In addition, a strain of *R. rubrum*, F24.1, has recently been isolated with an altered reaction center (181). This mutant is a spontaneous phototrophic revertant derived from a photosynthetically incompetent strain with a nonfunc-

tional reaction center. Strain F24.1 apparently lacks bacteriochlorophyll P800, a constituent of the reaction center (27, 174), but is, nevertheless, capable of photosynthetic growth. Picorel and co-workers (181) suggest that this mutant may be enriched in a second kind of reaction center which does not contain P800 and which is present as a minor component in wild-type cells. Such an explanation would reinforce previous proposals (236, 256) that two different kinds of reaction center coexist in membranes of *R. rubrum*. Alternatively, the reaction center of strain F24.1 may be modified so as to render P800 unnecessary. Indeed, if this is the case, studies with such mutants should further resolve the precise role of P800 in bacterial photosynthesis.

Temperature-sensitive mutants. Temperature-sensitive lesions of the photosynthetic apparatus of *R. rubrum* provide strains conditionally unable to perform photosynthetic functions associated with electron flow. Such mutants were selected by the phototactic enrichment technique, assuming that the phototactic response of photosynthetic cells relies on a properly functioning electron transport system (266). Other temperature-sensitive mutants of *R. sphaeroides* have been isolated (unpublished data) which are unable to grow aerobically at the nonpermissive temperature. The exact nature of the lesions affecting these strains is unknown.

The use of temperature-sensitive mutants, particularly in essential functions, has paid undoubted dividends in studies of other biological systems. It is perhaps surprising, therefore, that there has been a dearth of reports of investigations involving similar mutations in the photosynthetic bacteria. In particular, studies with temperature-sensitive mutants of the *Rhodospirillaceae* should facilitate identification of electron transfer components which may be common to both the respiratory and the photosynthetic electron transfer systems. The notion of shared electron transport components in these organisms is supported by several workers (see Towards Elucidation of Electron Transport Systems). Mutations affecting such components might reasonably be expected to be lethal during dark aerobic growth or photosynthetic growth. (When cells are grown anaerobically in darkness the components may be dispensable [277], and hence the mutations would not prove lethal.) Thus, the isolation of appropriate temperature-sensitive mutants should enable inroads to be made towards defining interrelationships of photosynthesis and respiration in the purple nonsulfur bacteria.

Morphological mutants. Vibrio (158) and bacilliform (155) mutants of *R. rubrum* have been described which apparently result from defects in D-alanine metabolism (156, 157).

The vibrio mutants were initially selected as strains resistant to D-cycloserine (an analog of D-alanine) (158). The phenotype of these mutants is evidently a consequence of perturbations in cell envelope biosynthesis.

Miscellaneous mutants. Certain mutants of *R. rubrum* have been selected on the basis of pigmentation after prolonged growth anaerobically in the dark (250). One mutant, strain C, synthesized bacteriochlorophyll *a*, altered membrane structures, and chromatophores during dark growth. Furthermore, strain C was capable of growing anaerobically in the light. In contrast, a second mutant, strain G1, was light sensitive and produced only trace amounts of bacteriochlorophyll.

Typically, wild-type strains of *R. capsulata*, unlike strains of *R. sphaeroides* and *R. palustris*, are unable to utilize glycerol as a carbon source (257). However, a spontaneous variant of *R. capsulata*, strain L1, capable of using glycerol for both anaerobic photosynthetic growth and aerobic dark growth, has been isolated (132). Two enzymes, glycerokinase and glycerophosphate dehydrogenase, not detectable in the parent, were found to be synthesized constitutively in this mutant (131, 132). By contrast, such enzymes are inducible, in the presence of glycerol, in *R. sphaeroides* (182). Constitutive synthesis of these enzymes in the mutant possibly reflects derepression in strain L1 of an operon not normally expressed in the wild type.

Mutants of *R. palustris* have been reported that differ from wild-type strains in that they are incapable of growing aerobically at the expense of cyclohexanecarboxylic acid or pimelate. Such mutants have been exploited in determining reactions involved in the photometabolism of benzoate by *R. palustris* (83).

Bacteriochlorophyll Biosynthesis and Related Phenomena

Elucidation of reactions involved in bacteriochlorophyll biosynthesis has depended largely upon the analysis of tetrapyrrole pigments accumulated by strains of purple nonsulfur bacteria in which bacteriochlorophyll biosynthesis is deranged by mutation or metabolic inhibitors. Figure 1 outlines reactions involved in bacteriochlorophyll biosynthesis and incorporates the mutational blocks for a series of mutants of *R. sphaeroides*. It is noteworthy that the precursor accumulated by *R. sphaeroides* strain 8 (see Table 1) does not fit into the scheme per se and may be indicative of an alternative pathway to

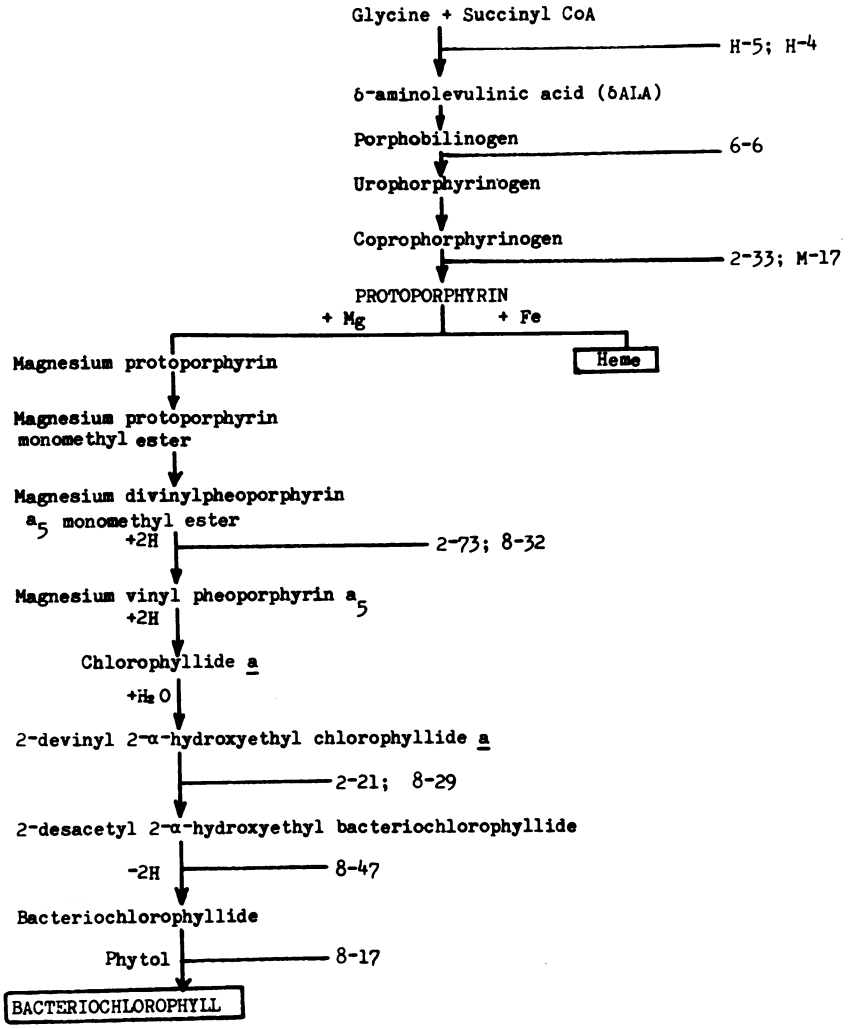

FIG. 1. *Scheme for heme and bacteriochlorophyll biosynthesis in R. sphaeroides (modified from Lascelles [119]). The mutational blocks in a number of strains of R. sphaeroides are indicated.*

bacteriochlorophyll in this organism (see reference 184). Mechanisms regulating bacteriochlorophyll biosynthesis have been proposed largely on the basis of the behavior of appropriate mutants under various environmental conditions. A brief review has recently appeared (119). δ-Aminolevulinate synthase represents one control locus, presumably regulated, at least in part, by the intracellular heme concentration (122). Magnesium chelatase, which appears to be critically sensitive to oxygen, is of particular importance in regulating the magnesium branch of the pathway (121). Certain of the biosynthetic enzymes appear to be subject to repression in the presence of oxygen. Mutants of *R. sphaeroides* have been isolated that continue to synthesize bacteriochlorophyll under conditions of high aeration (123). Presumably, this response is attributable to a derepression of synthesis of certain enzymes of the magnesium path under conditions normally causing their repression. It has been speculated that synthesis of all the enzymes of the magnesium branch of the pathway may be controlled by a regulatory gene which is in turn influenced directly or indirectly by oxygen (123).

Cohen-Bazire et al. (37) advanced a hypothesis, referred to as the "redox-governer" hypothesis, to account for the almost immediate cessation of bacteriochlorophyll biosynthesis in response to oxygen. It was suggested that the rate of bacteriochlorophyll and carotenoid biosynthesis was governed by the state of oxidation of a carrier in the electron transport system. This notion has subsequently been superseded in

light of observations with specific mutants of *R. capsulata* impaired in respiratory electron transport (139). It is envisaged that an oxygen-sensitive factor regulates bacteriochlorophyll synthesis. This factor, inactivated by oxygen, can be reactivated by a flow of electrons from the electron transport system, diverted possibly at the level of cytochrome *c*. The factor may represent one or more of the enzymes directly involved in bacteriochlorophyll synthesis or an effector molecule that interacts with them (139) (see Fig. 2). The involvement of cytochrome *c* could be tested for by investigating regulation of bacteriochlorophyll synthesis in mutants blocked in electron transport between cytochromes *b* and *c*.

An inverse correlation appears to exist between the intracellular concentration of adenosine 5'-triphosphate and the rate of bacteriochlorophyll biosynthesis in certain photosynthetic bacteria (62, 209). Furthermore, it has been proposed (62) that the amount of adenosine 5'-triphosphate within cells of *R. sphaeroides* is in itself decisive in modulating bacteriochlorophyll synthesis.

Ultrastructure studies with mutants blocked at specific stages in bacteriochlorophyll biosynthesis reveal that synthesis of the entire bacteriochlorophyll molecule is a prerequisite for assembly of the intracytoplasmic membrane system characteristic of pigmented cells (19, 165).

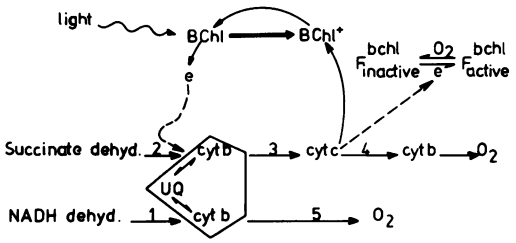

FIG. 2. *Model of electron transport pathways present in membranes of R. capsulata, incorporating a possible scheme for the regulation of bacteriochlorophyll synthesis by molecular oxygen (modified from Marrs and Gest [139] and La Monica and Marrs [115]). Both respiratory and light-driven electron flow systems are indicated. The numbered arrows represent steps in the respiratory electron transport pathways. The mutational blocks in respiration-deficient strains of R. capsulata are as follows: strain M1 is blocked in step 1; M2 is blocked in steps 1 and 2; M3 is blocked in step 2; M6 is blocked in step 5; M7 is blocked in step 4 by virtue of lacking the associated cytochrome b. Abbreviations: BChl, bacteriochlorophyll; UQ, ubiquinone; cyt, cytochrome; e, electrons; dehyd., dehydrogenase; NADH, reduced nicotinamide adenine dinucleotide. F^{bchl} represents a postulated O_2-sensitive factor required for BChl synthesis (139).*

In support of this are observations (28, 164, 165, 238, 239) which indicate an obligatory coupling between bacteriochlorophyll biosynthesis and the formation of specific chromatophore proteins. The role of the bacteriochlorophyll molecule in this process remains obscure. Possibly, the pigment exerts its effect at the level of transcription or translation. Alternatively, the bacterichlorophyll molecule may be necessary for assembly of these specific proteins into the architecture of the membrane (119, 239).

Analysis of glycerol auxotrophs of *R. capsulata* indicated a dependence of bacteriochlorophyll and carotenoid biosynthesis on phospholipid synthesis (108). An increased lipid content is associated with pigmented cells. It is not known whether lipid synthesis exerts direct regulatory control on carotenoid synthesis or whether a slow-down in carotenoid synthesis is a secondary effect of decreased bacteriochlorophyll production.

Clearly, more investigations at the genetic level are required to clarify the regulatory mechanisms involved in photopigment biosynthesis.

Towards Elucidation of Electron Transport Systems

The intracytoplasmic membrane of purple nonsulfur bacteria accommodates both the respiratory and the photosynthetic electron transport systems. Resolution of the precise nature and arrangement of components of either of these systems is thus complicated by their dual occurrence in the membrane. A promising approach to the analysis of these systems involves the use of mutants with lesions specifically affecting photosynthetic or respiratory competence. In addition, mutants with altered carotenoid patterns (notably, green, blue-green, and albino strains) have been widely exploited in monitoring electron transfer reactions (for example, 38, 57, 100, 204). These mutants have the advantage of permitting spectroscopic observation of electron transport components (for example, cytochromes) in the spectral region normally masked by the absorbance of photopigments characteristic of wild-type strains.

A series of respiration-deficient mutants of *R. capsulata*, including strains with depressed nicotinamide adenine dinucleotide, reduced form, and/or succinate dehydrogenase activities (strains M1, M2, and M3 [138]) and those with defects in the terminal portion of the electron transport system (strains M4, M5, M6, and M7 [138]), selected through the use of the "Nadi reaction" (105), have been investigated (115, 138, 139, 141, 278–280). It is inferred from the growth characteristics of such mutants that reduced

nicotinamide adenine dinucleotide dehydrogenase activity is essential to the aerobic competence of the organism, whereas succinate dehydrogenase activity is not (138, 141). The responses of these mutants, particularly to conventional inhibitors of electron flow, are compatible with a branched respiratory electron transport system for *R. capsulata* (Fig. 2), with two distinct terminal oxidases (115, 138, 279, 280). A high-potential, membrane-bound, *b*-type cytochrome (E_0' = +413 mV) found in aerobically grown cells of *R. capsulata* is apparently involved in cytochrome *c* oxidase activity (278, 279). A further high-potential *b*-type component (E_0' = +270 mV) which interacts strongly with carbon monoxide has been proposed as the true *o*-type oxidase of *R. capsulata* (280). *b*-Type components of similar oxidation-reduction potential to these have also been identified in aerobically grown cells of an albino mutant (strain V-2) of *R. sphaeroides* (205). Moreover, the *a*-type cytochrome which develops in *R. sphaeroides* during aerobic growth (107) has been partially characterized. Potentiometric titration at 607 nm revealed two components with oxidation-reduction midpoint potentials similar to those of eucaryotic cytochrome oxidase (E_0' = +375 mV and E_0' = +200 mV) (204) in membranes from strain V-2 of *R. sphaeroides*. Of all the members of the *Rhodospirillaceae*, the *a*-type cytochrome remains exclusive to *R. sphaeroides*.

There is speculation that certain electron transfer components are common to both the respiratory and the photosynthetic electron transport systems of *R. capsulata* (67, 115, 138, 279). The possibility of shared components has previously been suggested by the studies of Connelly et al. (38) and Jones and Plewis (102) with mutants of *R. sphaeroides*. Interrelationships between photosynthetic and respiratory electron transfer systems will be further resolved with the isolation and analysis of more mutants. In this connection, a mutant of *R. capsulata* blocked in electron transport between cytochromes *b* and *c* is currently being investigated (B. L. Marrs, private communication).

Other lesions responsible for respiratory deficiency in purple nonsulfur bacteria have been reported. Wittenberg and Sistrom (272) have isolated a mutant of *R. sphaeroides*, strain 37, incapable of growing aerobically in the dark except when the oxygen tension is low enough to permit photopigment synthesis. This is analogous to the behavior of certain reputedly "obligately anaerobic" photosynthetic bacteria (178). Possibly, the biochemical defect in such naturally occurring obligate phototrophs may be identical with that of *R. sphaeroides* strain 37. It has been proposed (272) that heme synthesis in strain 37 is obligatorily coupled to bacteriochlorophyll synthesis, implying some alteration in the normal regulatory mechanisms for synthesis of electron transport components. Studies with additional aerobically incompetent mutants may well provide a molecular explanation for the differential response of photosynthetic bacteria to molecular oxygen.

del Valle-Tascón et al. (44) have isolated mutants of *R. rubrum* which are incapable of phototrophic growth. One such mutant, strain F11, exhibits normal rates of endogenous cyclic photophosphorylation but is defective in photooxidase activity. Such observations suggest that the constituent(s) altered by mutation does not belong to the cyclic photophosphorylation system. The electron transfer step deranged in strain F11 is supposedly located on the low-potential side of the photosynthetic reaction center, between the primary electron acceptor and oxygen (45). Results from studies on the photooxidation of exogenous electron donors and of reaction center bacteriochlorophyll by chromatophores from mutant F11 are consistent with a branched model for light-driven electron transfer in chromatophores of *R. rubrum* (Fig. 3) (45). It is tentatively proposed that specific constituents of the photooxidase system are located in a side chain which connects a pool of cyclic electron acceptors with oxygen. Strain F11 is blocked in this side chain and is consequently deficient in photooxidase activity. The photooxidase system is apparently essential for the normal photosynthetic metabolism of *R. rubrum*, although its precise physiological role in vivo requires verification.

Mutants blocked in bacteriochlorophyll biosynthesis provide appropriate test systems for

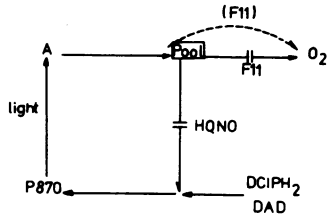

FIG. 3. *Model of light-driven electron transport in isolated chromatophores of R. rubrum (after del Valle-Tascón et al. [45]). Strain F11 is blocked in a side chain which connects a pool of secondary acceptors and oxygen. The dashed arrow represents an alternative site for oxygen reduction in this mutant. Abbreviations: HQNO, 2-heptyl-4-hydroxyquinoline-N-oxide; DAD, 2,3,5,6-tetramethyl-p-phenylenediamine; DCIP, 2,6-dichlorophenolindophenol; A, primary acceptor; P870, reaction center bacteriochlorophyll.*

monitoring the contributions of specific components to the reconstitution of photosynthetic activity and hence provide information concerning the assembly of the photosynthetic apparatus. Reconstitution of photosynthetic reactions has been demonstrated with the bacteriochlorophyll-lacking membranes of aerobically grown cells of mutants of *R. sphaeroides* (102) and *R. capsulata* (67, 68) when supplemented with reaction center bacteriochlorophyll. The additional effect of light-harvesting chlorophyll on the "reconstituted" system has been studied in *R. sphaeroides* (96). It has been suggested, at least for *R. sphaeroides*, that the respiratory electron transport system is of similar composition and orientation to the photosynthetic electron transport system. Terminal oxidases or reaction center complexes may thus be incorporated into a preexisting photosynthetic or respiratory electron transport chain, depending on the mode of growth (101, 102). Other mutants (and, in particular, those specifically lacking reaction center bacteriochlorophyll, but not the antenna chlorophyll) should add a further refinement to the reconstitution system.

Recently, anaerobic dark growth of *R. capsulata* has been demonstrated with glucose as the carbon source, but only in the presence of dimethyl sulfoxide (277). In this respect *R. capsulata* apparently differs from other members of the *Rhodospirillaceae*, namely, *R. palustris*, *R. sphaeroides*, and *R. rubrum*, which do not require dimethyl sulfoxide for fermentative anaerobic growth in darkness (251). A series of mutants of *R. capsulata*, including photosynthetically or aerobically incompetent strains, were examined for the ability to grow under anaerobic conditions in the dark (277). Results indicated that the bacteriochlorophyll-mediated energy conversion system of *R. capsulata* is unnecessary for anaerobic dark growth. Furthermore, neither reduced nicotinamide adenine dinucleotide dehydrogenase activity nor either of the terminal respiratory oxidases is essential for anaerobic growth in darkness. However, although the entire respiratory chain is apparently not required, certain cytochromes may be needed for reduction of the dimethyl sulfoxide. It is proposed that *R. capsulata* requires a terminal electron acceptor for anaerobic dark growth and that dimethyl sulfoxide can serve the purpose.

The preceding sections amply illustrate the importance of a combined biochemical and genetic approach in the elucidations of electron transfer systems and of reactions involved in bacteriochlorophyll biosynthesis. Providing that the effects of mutation are strictly localized and do not excessively perturb the system under investigation, valid extrapolation can be made to the situation appertaining in wild-type cells. Theoretically, appropriate classes of mutants coupled to efficient gene transfer systems should permit a thorough analysis of photosynthetic processes in the *Rhodospirillaceae*.

GENETIC ORGANIZATION

The base composition of DNA from members of the *Rhodospirillaceae* ranges from 60 to 67 mol% guanine plus cytosine (G+C) for *Rhodospirillum* species, 64 to 70 mol% G+C for *Rhodopseudomonas* species, and 62 to 65 mol% G+C for *Rhodomicrobium vannielii*, as estimated from thermal denaturation profiles, density gradient centrifugation, and ultraviolet spectrophotometry (93, 177, 215). The G+C content of DNA from purple sulfur bacteria (*Chromatium* species) is from 48 to 70 mol%, whereas the value for green sulfur bacteria (*Chlorobium* species) is lower (from 50 to 58 mol% G+C) (93, 177) (Table 2). By contrast, there is considerable variation in the G+C content of DNA in the cyanobacteria (from 35 to 70 mol%) (273).

The genome size of the purple nonsulfur bacterium *R. sphaeroides* is about 1.6×10^9 daltons (75), a value comparable to that of other bacteria. On the other hand, the genome sizes of a number of cyanobacteria, determined from renaturation kinetics, range from approximately 2×10^9 to 7×10^9 daltons and appear to fall into four distinct groups (90). In fact, the largest of these genomes are amongst the most complex reported for procaryotes. Further, the increase in genetic complexity coincides with increasing morphological and biochemical complexity within the cyanobacteria (90). Certain cyanobacteria apparently contain multiple copies of their genome per cell (192, 273). Moreover, at least some photosynthetic procaryotes contain extrachromosomal (covalently closed circular [CCC]) DNA in addition to the chromosome

TABLE 2. *Base composition (moles percent G+C) of DNA of some photosynthetic bacteria*

Species	mol% G+C of total bases[a]	Reference
Chlorobium spp.	51–58	93, 177
Chromatium okenii	48–50	133
Chromatium gracile	68–70	133
R. vannielii	62–65	177, 215
R. capsulata	65–67	177, 215
R. sphaeroides	66–70	215
Rhodopseudomonas viridis	67–68	215
R. rubrum	62–65	215

[a] A range of values for moles percent G+C is given resulting from the different methods used (see text).

(see Extrachromosomal Deoxyribonucleic Acid).

It has been reported for certain purple nonsulfur bacteria (78, 125, 140, 194) and for the cyanobacterium *Anacystis nidulans* (51) that the ribosomal RNA (rRNA) complement is atypical. There is apparently no stable 23S rRNA component. The 23S rRNA is considered to be a precursor molecule which is subsequently cleaved into two smaller stable rRNA species (51, 78, 140, 194). This has implications for the role of rRNA and raises questions as to the relationship between rRNA cleavage and ribosome function in these organisms.

In passing, not much is known about DNA replication in relation to the cell cycle in the *Rhodospirillaceae*. Studies of Westmacott and Primrose (268) on the effect of nalidixic acid on the cell cycle of *R. palustris* indicate a dependence of cell division and flagellum and holdfast syntheses on the completion of chromosome replication. However, photosynthetic membrane formation and wall extension are apparently independent of chromosome replication. In addition, pre- and postsynthetic gaps accompany a round of DNA replication in *R. palustris*. Such correlation between cell division and DNA replication has previously been reported for other organisms, notably, *Escherichia coli* (for example, 22, 25, 50). However, coupling between the termination of DNA replication and cell division is not a universal occurrence in bacteria. Indeed, in the cyanobacterium *A. nidulans* initiation of DNA replication appears to be a necessary event for cell division to occur (134, 135).

EXTRACHROMOSOMAL DEOXYRIBONUCLEIC ACID

Occurrence

Extrachromosomal (plasmid) DNA is commonly found in bacteria and determines a diversity of biological functions (for reviews, see references 31, 61, 147, 160–162, 186, 269). There are reports of the presence of plasmid DNA in both photosynthetic bacteria (74, 75, 206, 235) and cyanobacteria (10, 187, 193; D. Heaton and E. W. Frampton, Abstr. Annu. Meet. Am. Soc. Microbiol. 1976, I117, p. 131).

Suyama and Gibson (235) reported the presence of plasmid DNA in *R. sphaeroides*. Despite the failure of other workers (152) to detect such DNA in this organism, these initial observations were later substantiated by Gibson and Niederman (75), who, furthermore, detected not one, but two, species of plasmid DNA of similar molecular weights (70×10^6 to 75×10^6) but of different buoyant densities (1.718 and 1.724 g/cm^3) in *R. sphaeroides* strain NCIB 8327. Recent work of Saunders and colleagues (206) supported and extended these observations. Three CCC species of extrachromosomal DNA were identified by electron microscopic analyses (Fig. 4) in both aerobically and photosynthetically grown cells of *R. sphaeroides* strain 2.4.1. Molecular weights of these plasmids, as determined from contour length, were 75×10^6, 66×10^6, and 28×10^6 for *R. sphaeroides* strain 2.4.1. Plasmids weighing 28×10^6 and 66×10^6 daltons were of a buoyant density of 1.717 g/cm^3, and those weighing 75×10^6 daltons were of a buoyant density of 1.724 g/cm^3. A photosynthetically incompetent strain of *R. sphaeroides*, SLS I, selected after treatment of cells of strain 2.4.1 with sodium lauryl sulfate, also contained three species of plasmid DNA. The molecular weights of the two larger plasmids were identical with those of strain 2.4.1. The molecular weight of the third plasmid of strain SLS I was significantly larger (34×10^6). It has been tentatively proposed (206) that the increased size of this plasmid derives from some kind of gene duplication and/or rearrangement. Such a modification could arise by integration of an insertion sequence(s) with concomitant loss of gene function (154, 230). This increased size of a plasmid species is not a general property of photosynthetically incompetent (Pho^-) strains of *R. sphaeroides*, since the plasmid complement of another Pho^- strain, obtained after nitrosoguanidine mutagenesis, was identical with that of strain 2.4.1 (206).

Plasmid DNA has been detected in other photosynthetic bacteria, including *R. capsulata* (Hu and Marrs, private communication; V. A. Saunders, unpublished data) and *Chromatium* D (235). *R. capsulata* apparently contains species of CCC DNA of 70×10^6 and 100×10^6 daltons, as estimated from sucrose gradient sedimentation analysis (Hu and Marrs, personal communication).

Of the cyanobacteria, *A. nidulans* has been reported to contain plasmid DNA of about 28×10^6 to 33×10^6 daltons, which is present as at least seven to eight copies per genome equivalent (Heaton and Frampton, Abstr. Annu. Meet. Am. Soc. Microbiol. 1976, I117, p. 131; E. W. Frampton, private communication). Analyses of the plasmid DNA of *Agmenellum quadruplicatum* by electron microscopy and agarose gel electrophoresis have revealed a number of discrete classes of DNA circles, ranging in molecular weight between 3×10^6 and 65×10^6 to 80×10^6 (193). The CCC DNA in this organism was equivalent to about 5% of the total cellular DNA. The presence of multiple classes of CCC DNA within a procaryotic cell is not without precedent (see, for example, reference 149). It has yet to be

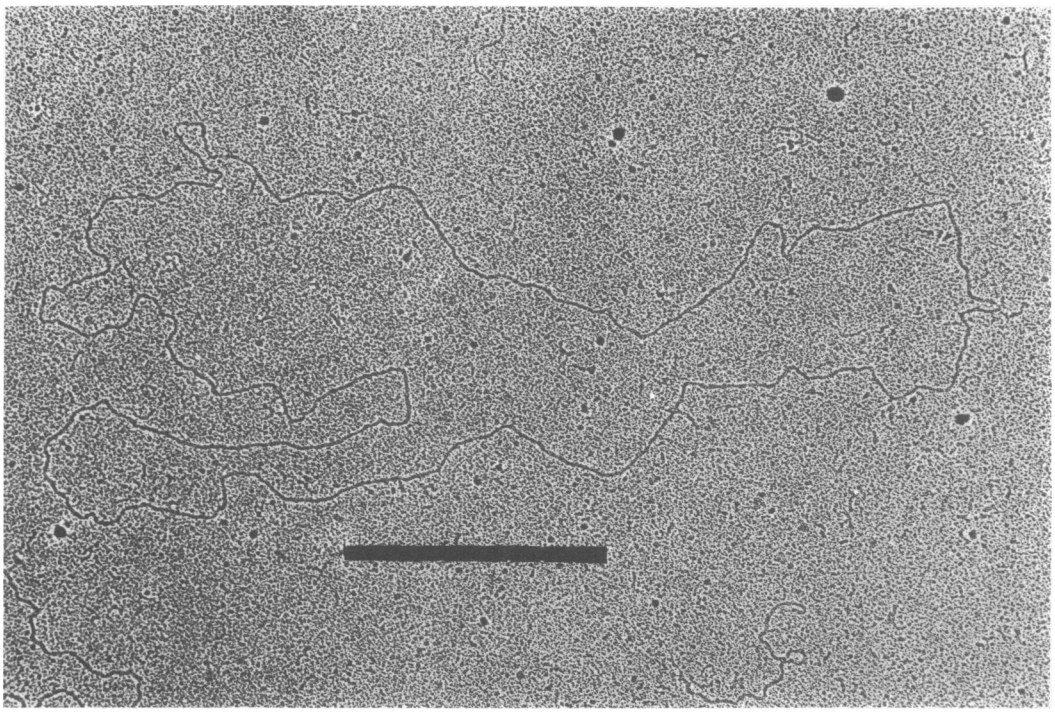

FIG. 4. *Electron micrograph of extrachromosomal DNA from R. sphaeroides (from Saunders et al. [206]). Circular DNA of 28 × 10^6 daltons isolated from strain 2.4.1 is shown. Bar = 1 μm.*

established whether plasmids are ubiquitous within the photosynthetic procaryotes.

Functions Evaluated

The nature of the information encoded by plasmid DNA in photosynthetic procaryotes remains largely a matter for conjecture. By analogy with the plastid DNA of eucaryotic plant cells, it has been suggested that the plasmid DNA may have a role in specifying the photosynthetic apparatus (75). However, naturally occurring plasmids are generally dispensable in procaryotes (160, 162). Thus, essential biological functions, presumably including photosynthetic activity in this case, are unlikely to be plasmid determined. Furthermore, no transcriptional specificity between the RNA from aerobically or photosynthetically grown cells has been demonstrated in *R. sphaeroides* and *R. rubrum* by using both chromosomal and extrachromosomal DNA as DNA-RNA hybridization probes (24, 77, 271, 274). Irrespective of the gross structural differences and the variation in enzyme patterns (118) associated with growth of these organisms in different atmospheric milieus, no qualitative differences are obvious between the RNA species of aerobic and photosynthetic cells (24, 64, 271, 274). However, there does appear to be some difference in the stability of an RNA component under aerobic and anaerobic conditions (270). These observations led to the idea that a translational mode of regulation of protein synthesis may exist for these bacteria (24, 270, 271, 274).

Possible genetic functions for the plasmid DNA of *R. sphaeroides* have been evaluated by Saunders et al. (206). Part of the plasmid DNA complement may be composed of temperate phage. Indeed, several temperate bacteriophages have been isolated from strains of *R. sphaeroides* (153), though no infective phage particles have been detected in cultures of strain 2.4.1. Recently, putative viral R plasmids have been reported for a number of *R. sphaeroides* isolates (176). These strains were resistant to penicillin, by virtue of a diffusible penicillinase, and carried between one and three prophages. Bacteriophages released by such strains were active against derivatives of these strains which had been "cured" of prophage. Furthermore, resistance to penicillin could be transferred at high frequency to susceptible recipients. However, generalized transduction mediated by these phages could not be demonstrated. The penicillinase-producing strain *R. sphaeroides* RS601 released the bacteriophage designated Rφ6P spontaneously. The DNA extracted from bacteriophage Rφ6P was circular DNA of 33 (±2) × 10^6 daltons (176), a value close to that of the smallest plasmid of *R. sphaeroides* strain 2.4.1

(cf. reference 206). It has been suggested (176) that a gene for penicillinase production is carried as part of the wild-type bacteriophage genome and that this genome exists as an extrachromosomal element in these lysogenic strains. The carriage of transposable resistance genes by bacteriophages has been demonstrated in the laboratory in the *Enterobacteriaceae* (15, 76). However, this appears to be the first report of a bacteriophage isolated from the wild which apparently carries antibiotic resistance genes.

An isolate of *R. capsulata*, strain SP108, similarly produces a diffusible penicillinase which confers considerable resistance to penicillin on this strain (267). This contrasts with the extreme susceptibility of classical laboratory strains of *R. capsulata* to this antibiotic. Indeed, the great susceptibility of many strains of *R. capsulata* to penicillin G is a feature which distinguishes this species from closely related members of the *Rhodospirillaceae* (267). The penicillin-inactivating enzyme of strain SP108 is apparently an inducible β-lactamase, with a marked preference for benzylpenicillin as a substrate (V. A. Saunders, manuscript in preparation). Furthermore, resistance to penicillin in strain SP108 is lost at a relatively high frequency (267; unpublished data), which would be consistent with a plasmid-specified character (160).

It is perhaps noteworthy at this juncture that photosynthetic bacteria are sometimes isolated from stagnant ponds which have been contaminated with farm effluents (see, for example, 1, 142, 153, 267). This may provide localized concentrations of antibiotics derived from, for example, animal feed and a reservoir of bacteria capable of acting as donors of antibiotic resistance genes.

Penicillinase (β-lactamase) production has also recently been reported for certain cyanobacteria, in particular *Anabaena* sp. (strain 7120) and *Coccochloris elabens* (strain 7003) (114). Penicillin did not appear to induce penicillinase production in these organisms. Furthermore, the enzymes from these strains were more active on penicillins than on cephalosporins, thereby resembling the "type II" enzymes of gram-negative bacteria (190).

The production of penicillinases by photosynthetic procaryotes poses fundamental questions as to the nature and origin of the penicillinase gene(s). For instance, do these enzymes correspond to those widely distributed amongst the enteric bacteria, *Pseudomonas* and *Haemophilus* (87, 202)? Of particular interest in this respect is the type IIIa (TEM) β-lactamase determined by transposon *A* (86). Transposon *A* is capable of translocation from one replicon to another and thus may be a significant contributor to the prevalence of antibiotic resistance amongst bacteria (33, 200). It is likely that some disparity in genetic composition will exist between common laboratory strains isolated some 20 or more years ago and those recently obtained. Increased levels of pollutants, including antibiotics and heavy-metal ions, have undoubtedly had dramatic effects on the genetic constitution of bacterial populations in general (see, for example, references 130, 186, 189). Thus, photosynthetic procaryotes will, in all certainty, acquire resistance genes to protect themselves against such pollutants. In turn, this should conveniently provide naturally marked derivatives of these organisms for use in genetic experiments.

BACTERIOPHAGE AND BACTERIOCINS

Isolation and Characterization of Bacteriophage and Cyanophage

The value of transduction in the provision of fine-structure genetic maps and the construction of specific mutant strains of bacteria is indisputable (see, for example, references 12, 94, 199, 231, 243, 246). The quest for corresponding phage-mediated gene transfer systems within the photosynthetic procaryotes has promoted studies on the virology of these organisms.

The first report of a virulent phage specific for a member of the *Rhodospirillaceae* described phage Rp1 of *R. palustris* (66). Both virulent and temperate phages specific for *R. sphaeroides* (1, 153) and *R. capsulata* (208, 263) have subsequently been isolated and characterized. Their properties have recently been documented in detail (143). In addition, temperature-sensitive mutants of the phage RC1 of *R. capsulata* have been obtained (261). Thus far, however, no bona fide transduction has been reported involving any of them. More promising are the results with certain phages of *R. sphaeroides* recently isolated by Kaplan and colleagues (S. Kaplan, private communication). Phage-mediated transfers of antibiotic resistance and nutritional markers have been achieved between strains of *R. sphaeroides*, albeit at fairly low transfer frequencies. Although these results are preliminary, it is conceivable that with further refinements such a transducing system will prove suitable for exploring the genome of *R. sphaeroides*.

First reports of viruses attacking and lysing species of the cyanobacteria were those of Safferman and Morris (196). Several viruses (cyanophages) have since been characterized, and there is considerable documentation of their morphology, physiology, and ecology (for example, 172, 195, 212, 273). However, their role as mediators of genetic exchange remains unproven. Temper-

ature-sensitive mutants of the cyanophage LPP2-SP1, which lysogenizes *Plectonema boryanum*, have been isolated, and a linkage map of the phage has been constructed based on recombination between mutants in two-point crosses (191).

In addition to genetic considerations, host-bacteriophage interactions necessarily relate to host cell physiology and, in turn, provide information on fundamental aspects of bacteriophage replication and assembly (2, 34, 231). In this regard, photosynthetic procaryotes undoubtedly offer distinct advantages over other procaryotes, primarily because the energy status of the host cell can be conveniently manipulated merely by adjusting such parameters as light intensity. Schmidt et al. (208), investigating the bioenergetics of bacteriophage RC1 replication in *R. capsulata*, concluded that the energy requirement for the replication of this phage is more critical than that for uninfected host cell growth. In photosynthetically grown host cells, phage RC1 replication could be supported either by photophosphorylation or oxidative phosphorylation. However, in aerobically grown host cells, phage multiplication was supported by oxidative phosphorylation; the anaerobic photophosphorylation capacity of such cells would not suffice. Clearly, in aerobically grown cells development of the photosynthetic pigment system is drastically suppressed (118). Therefore, such cells are severely limited in photosynthetic energy conversion capacity. The required photophosphorylation capacity for phage development can only be achieved in aerobically grown cells which contain a sufficient quantity of bacteriochlorophyll (0.6 μg/mg of dry weight) before phage infection. Once phage has infected aerobic cells, subsequent synthesis of the photophosphorylation system is prevented when cells are incubated under anaerobic conditions in the light. Phage RC1 infection apparently interferes with synthesis of both bacteriochlorophyll and protein in *R. capsulata*. It is proposed (208) that the infecting phage is entirely dependent on the temporal energy conversion activity of the host and that a relatively high rate of adenosine 5'-triphosphate regeneration is required for proper expression of the viral genome.

The characteristics of infection of *R. sphaeroides* by phage RS1 indicate that some form of physiological specificity exists (1). Anaerobically grown cells of *R. sphaeroides* strain 2.4.1 are apparently less susceptible to such infection than are aerobically grown cells (the adsorption rate constants of RS1 are 1.2×10^{-9} ml/min to aerobic cells and 0.58×10^{-9} ml/min to anaerobic cells). This could reflect differences between these two cell types in cell surface properties and/or the intracytoplasmic membrane system such that the adsorption and/or penetration process is hampered in anaerobically grown cells (1). Once effective penetration of such cells has occurred, the burst size is similar to that observed during aerobic infection (15 to 20 plaque-forming units per cell).

Bacteriophage Rϕ-1 is a temperate phage specific for *R. sphaeroides* (153). It was isolated from the prophage state by induction with mitomycin C. *R. sphaeroides* strain 2.4.1 is not susceptible to infection by Rϕ-1. However, mutant derivatives of the phage have been isolated which can form plaques on strain 2.4.1. Interestingly, the original phage Rϕ-1 is chloroform susceptible, whereas the mutant is chloroform resistant. The growth pattern of the phage is similar whether it begins its life cycle by induction or infection. Furthermore, Rϕ-1 forms plaques with equal efficiency on susceptible host cells whether grown aerobically in darkness or anaerobically in the light.

The requirements for optimal replication of phage particles appear to vary. For example, in both *R. capsulata* (208) and the cyanobacterium *Nostoc muscorum* (4), optimal phage replication necessitates illumination throughout the latent period, whereas reproduction of cyanophage LPPI-G in *P. boryanum* requires illumination solely through the eclipse period (171). These different requirements may reflect intrinsic differences in metabolism of the particular host species.

Bacteriocinogeny

Recent surveys (82, 263) have revealed that representatives of the *Rhodospirillaceae* produce bacteriocins. *R. sphaeroides* and *R. palustris* exhibit few intraspecies-specific inhibitory interactions. Greatest inhibitory activity, both interspecies and intraspecies specific, was exhibited by strains of *R. capsulata*. In addition, it is noteworthy that purple nonsulfur bacteria produce antimicrobial substances which are not akin to bacteriocins but are metabolites extractable with organic solvents (104). Such antibiotic effects produced by *R. sphaeroides* (strain 1c7) are restricted to gram-positive bacteria, for example, *Bacillus subtilis*, whereas those produced by *R. capsulata* (strain FC101) appear to be unspecific. The precise natures of these antibiotic substances require elucidation. No phenomenon analogous to that of bacteriocinogeny has been reported in the cyanobacteria.

Bacteriocins are in themselves of interest from structural, functional, and evolutionary standpoints (85). Furthermore, their production is often determined by transmissible plasmids (85). Therefore, the possibility exists that if compa-

rable plasmids reside in members of the *Rhodospirillaceae*, they could be exploited as vehicles of genetic exchange. However, the location of the genetic determinants for bacteriocinogeny in these organisms remains obscure, and no associated gene transfer has so far been reported.

"GENE TRANSFER AGENT" OF *RHODOPSEUDOMONAS CAPSULATA*

Discovery and Properties

The first report of a genetic exchange system for a photosynthetic bacterium was that of Marrs (142) for *R. capsulata*. Various isolates of *R. capsulata* were screened for recombination of antibiotic resistance markers. Genetic exchange appeared to be mediated by a ribonuclease- and deoxyribonuclease-resistant vector produced specifically by strains of *R. capsulata* and thereafter designated the "gene transfer agent" (GTA) (142). Different isolates vary in their ability to donate and receive the GTA (263). Furthermore, strains receiving genetic information via the GTA do not themselves become GTA producers (143). Genetic transfer mediated by the GTA is limited to *R. capsulata* and does not extend to other members of the *Rhodospirillaceae* (263). Moreover, no comparable genetic exchange system has, to date, been discovered for other purple nonsulfur bacteria (263; unpublished data). Morphologically, the GTA particle resembles a small bacterial virus, with an icosahedral head, short spikes, and a tail (143). The nucleic acid of the GTA is linear double-stranded DNA of 3.6×10^6 daltons (143, 221), and the ultraviolet inactivation spectrum of the GTA is similar to that of bacterial viruses (222). However, the physical size of the GTA particle (70S [142]) is much smaller than that of any known transducing bacteriophage. Furthermore, no plaque-forming activity appears to be associated with the system, and there is no obvious correlation between the capacity of strains of *R. capsulata* to produce GTAs and their susceptibility to known bacteriophages (263). Kinetics of GTA release by a donor culture differ from those normally associated with phage production (cf. references 97, 144). GTAs are typically released in one or two abrupt waves towards the end of the exponential phase of growth (222). Whether cell lysis always accompanies this process has yet to be fully ascertained.

The gene transfer process in *R. capsulata* seemingly resembles generalized transduction. All regions of the bacterial genome thus far examined can be transferred, and transfer frequencies comparable to those for generalized transducing systems (4×10^{-4} "transferants" per recipient) can be achieved (222). Moreover, the transferred genetic markers appear to be stably inherited. Recombination is apparently accompanied by displacement of the corresponding resident marker (143). Analyses of the kinetics of renaturation (C_0t analysis) of the DNA contained in the GTA (Hu and Marrs, manuscript in preparation) indicate that more than 95% of this DNA is from the bacterial genome. Sequences complementary to the chromosomal and plasmid DNA of *R. capsulata* are found in the GTA, and it appears that all portions of the genome of *R. capsulata* are equally represented in the DNA of a population of GTA particles.

The precise nature of this gene transfer system remains enigmatic. Marrs and co-workers speculate that it may represent a "prephage" system (143, 222), in which case it is envisaged that a GTA-like system evolved in response to the selective advantage which the capacity for genetic exchange might confer. Thus, the GTA system could represent a precursor of the bacterial virus, rather than a derivative of a preexisting phage. Alternatively, the GTA may be a defective or cryptic phage capable of generalized transduction (222). This permits an equally plausible explanation to be inferred from the observations that the GTA has a limited ability to transfer 3×10^6 to 4×10^6 daltons of DNA (221) (presumably equivalent to approximately five to seven genes, if transcription of the genes is nonoverlapping). Phage particles of similar complexity to, albeit of larger size than, the GTA (for example, those of the T-even group) contain a genome of about 10^8 daltons (265). If, as seems likely, the genome size of the GTA itself were to exceed five to seven gene equivalents, then the head of the GTA would be unable to accommodate all the genetic information necessary to specify a mature GTA particle. Hence, GTA particles would, at best, carry only fragments of their own genetic complement. Accordingly, such particles would be nonlytic and lack overt viral activity. Furthermore, recipients of genetic material via GTAs would never become GTA producers unless, by chance, through multiple infections they simultaneously acquired all the genes necessary to specify GTA production. Even if the GTA particle could carry its genome in its entirety, failure to transmit GTA production to recipient cells could be explained if the genetic determinants for the GTA were scattered at various loci on the replicons resident in *R. capsulata*. Consequently, chances of incorporation of a complete GTA genome into a single particle during the encapsidation process would be drastically reduced. Possibly, this gene transfer system could be dissected by isolating from GTA-producing parent strains mutants impaired in GTA production. Such "GTA defec-

tive" strains could be used as recipients in genetic crosses with other GTA producers as donors. Restoration of the capacity to produce the GTA in transferants may allow the extent and map positions of the GTA determinants to be established. Certain mutants of *R. capsulata* have recently been isolated that are "overproducers" of the GTA (143). These strains may further resolve the nature of this genetic exchange system and, in particular, enable an estimate of how many genes are involved in specifying the GTA and their location in *R. capsulata*. However, there still remains the problem of screening for a characteristic for which there is no direct selection procedure and for which a biological assay is the sole means of detection.

The GTA system of *R. capsulata* has been used in manipulating genes specifying the photopigment system (54, 143, 263, 276) and the nitrogen fixation machinery (264). Moreover, specific mutant strains have been constructed, and the lesions characterizing others have been investigated with this genetic vehicle.

Transfer of genes for nitrogen fixation, via the GTA, to certain Nif^- mutants of *R. capsulata* results in acquisition by recipients of the dual ability to fix nitrogen and produce hydrogen (264). These findings support the proposal (170) that nitrogenase and hydrogen-evolving hydrogenase activities of purple nonsulfur bacteria are catalyzed by the same enzyme complex. Furthermore, this hydrogenase activity apparently differs from that associated with the utilization of hydrogen as an electron donor for photoautotrophic growth (264).

Restoration of photosynthetic competence to Pho^- mutants of *R. capsulata* has been effected with the GTA (54, 263). Drews and co-workers (54) demonstrated concomitant restoration of the abilities to synthesize bacteriochlorophyll and to form reaction center and light-harvesting proteins to *R. capsulata* mutants defective in these abilities. Analyses of various transferants suggest that reaction center proteins and light-harvesting complex I (128) form a structural unit in the intracytoplasmic membranes of *R. capsulata* (54). It has yet to be ascertained whether the genes specifying synthesis of these specific proteins of the photosynthetic apparatus and of bacteriochlorophyll are closely aligned on the genome of *R. capsulata*.

Mapping Genes for Bacteriochlorophyll and Carotenoid Biosynthesis

The GTA has been successfully exploited in conjunction with a series of mutants of *R. capsulata* in the construction of a map for genes determining bacteriochlorophyll and carotenoid production (276). One-, two-, and three-point and ratio test crosses were performed between various strains, and a new mapping function was derived to convert cotransfer data into map distances. Lacking *cis-trans* complementation data for this organism, it was assumed that a cluster of mutations giving the same phenotype represented a gene. Accordingly, clusters of mutations delineating seven genes, five affecting carotenoid biosynthesis and two affecting bacteriochlorophyll biosynthesis, have been arranged in one linkage group (Fig. 5). Mutations in either the *crtB* or *crtE* gene can give rise to the blue-green phenotype, whereas mutations in the *crtD* or *crtC* gene cause the green phenotype and those in the *crtA* gene cause a yellow phenotype. The loci *bchA* and *bchB* specify products necessary for reactions in bacteriochlorophyll biosynthesis. Linkage between these genes has possible implications for their coordinate expression at the transcriptional level. An interesting observation from the mapping studies was the apparently obligatory requirement for two specific mutations to obtain viable blue-green strains of *R. capsulata*: one lesion results in loss of colored carotenoids; the other (as yet of undefined map location) results in an alteration of the absorption spectrum of bacteriochlorophyll (54, 137, 143, 276). It has been suggested (137) that the mutation(s) responsible for alteration in the absorption spectrum of bacteriochlorophyll in fact blocks formation of light-harvesting bacteriochlorophyll complex II (128). If these mutations perforce accompany each other in blue-green strains, this could help to clarify the role(s) of carotenoids in photosynthetic bacteria.

TRANSFORMATION

So far, there has been no unequivocal demonstration of genetic transformation in the photosynthetic bacteria. By contrast, there are several reports of gene transfer by transformation in the cyanobacteria (see reference 43). Transformation in *A. nidulans* was first reported by Shestakov and Khyen (213). The process was mediated by chemically extracted DNA and was deoxyribonuclease sensitive. Subsequently, Herdman and Carr (91) described a transformation system for *A. nidulans* effected by an extracellular DNA:RNA complex. More extensive genetic linkage was observed in this process than in that mediated by chemically pure DNA. However, a mutagenic phenomenon appeared to be associated with the transformation process (whether with extracellular or chemically extracted donor DNA) (88, 89) which presumably interfered with accurate determination of linkage values in genetic mapping studies with *A. nidulans*. Nevertheless, it has been possible to exploit the mutagenic process per se in aligning

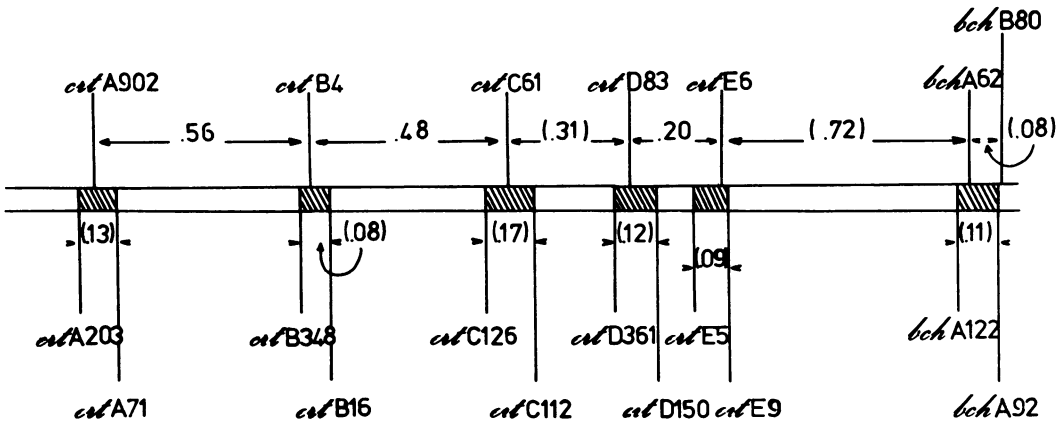

FIG. 5. *Genetic map of R. capsulata, indicating loci concerned with carotenoid and bacteriochlorophyll biosynthesis (from Yen and Marrs [276]). The numbers above the map represent the distances, in map units, between specific markers in each gene. The numbers below the map are estimates of the minimum length of each gene. Distances obtained by subtraction are given in parentheses.*

certain genetic markers, and recombination maps of *A. nidulans* have been constructed (43, 88, 89).

In addition to the intraspecies-specific transformation systems for *A. nidulans* (88, 89, 92, 148, 169, 213) and *Aphanocapsa* 6714 (11), an intergeneric transformation system has recently been reported for cyanobacteria (46). Intergeneric transfer of antibiotic resistance markers has been demonstrated from *A. nidulans* to *Gloeocapsa alpicola* and vice versa, in a process sensitive to both deoxyribonuclease and ribonuclease. Such genetic transfer across generic boundaries offers considerable scope for mobilizing genes (for example, those specifying nitrogen fixation) within the cyanobacteria.

Investigators' inability to develop a genetic transformation system for photosynthetic bacteria may be due to one or a number of contributory factors. First, the possibility exists that the donor nucleic acid may be inactivated by extracellular nucleases. This explanation does not, however, apply to *R. sphaeroides* strain 2.4.1, which apparently produces no extracellular deoxyribonuclease (unpublished data). Alternatively, the cell walls of purple nonsulfur bacteria may never achieve a competent state for taking up the DNA. Even if donor DNA could traverse the cell envelope, successful transformation with linear DNA would, presumably, still depend on a functional recombination system. The success of GTA-mediated gene transfer in *R. capsulata* and of R plasmid-directed gene transfer in *R. sphaeroides* (see below) implies that these organisms are recombination proficient. However, it is noteworthy that transfer of chromosomal markers by transformation in *E. coli* was initially hampered by the activities of the recombination exonuclease system (*recB/recC* exonuclease V) (166), which degraded the incoming linear "transforming" DNA. In contrast, linear DNA entering the cell by conjugation or transduction in *E. coli* is apparently refractory to such attack. It was only with subsequent mutational blocks in the *recB/recC* exonuclease, coupled with a suppressing mutation opening up a further minor recombination pathway, that effective transformation with chromosomal DNA was achieved in *E. coli* (166). Thus, the portal used in transformation may result in the genetic information being particularly vulnerable to nuclease attack. By analogy, whereas a recombination system is operative in certain members of the *Rhodospirillaceae*, it could equally act as a specific barrier to transformation in these organisms. Only when a greater understanding of the general genetics and, particularly, of recombination is available in the *Rhodospirillaceae* can such problems be resolved. Clearly, therefore, a useful approach in the development of a transformation system for the purple nonsulfur bacteria may be to use suitably marked plasmid (CCC) DNA as a probe in deriving potential competence regimes. This could circumvent any requirement for, or damage done by, recombination nucleases.

CONJUGATION

Transfer of genetic material by cell-to-cell contact has thus far not been observed to be indigenous to members of the *Rhodospirillaceae*. The presence in certain members of this group of plasmid DNA, which is of comparable size to the F factor of *E. coli*, prompted speculation that such plasmids may specify sex factor activity (75). However, genetic conjugation mediated by native plasmid species has not been observed in *R. sphaeroides* (206). Of course, this

may be merely a manifestation of intrinsically low transfer frequencies for chromosomal markers coupled with such phenomena as surface exclusion and incompatibility (201), if all strains used in the genetic crosses contain homologous sex factors.

On the other hand, *R. sphaeroides* and *R. rubrum* have been shown to act as recipients for the resistance (R) plasmid R1822 derived from *Pseudomonas aeruginosa*. However, the plasmid was unstable in these recipients in the absence of the appropriate selection pressures (167). Subsequently, W. R. Sistrom (private communication) has demonstrated transfer of the same plasmid to strains of *Rhodopseudomonas gelatinosa*. However, cotransfer of chromosomal genes has not yet been observed.

By contrast, current attempts to introduce other sex factors and, notably, further plasmids of the P incompatibility (IncP) group (20, 40, 162) into these organisms are more encouraging. Kaplan (private communication) and co-workers can demonstrate stable transfer of several R plasmids from *E. coli* to *R. sphaeroides* and subsequently between strains of *R. sphaeroides*. Concomitant intraspecies transfer of chromosomal markers, for example, antibiotic resistance and nutritional markers, has been achieved for *R. sphaeroides*.

Recently, Sistrom (217) has accomplished stable transfer of the R plasmid R68.45 (84, 109) from *P. aeruginosa* (strain PAO25 [R68.45]) to strains of *R. gelatinosa* and *R. sphaeroides*. The frequency of transfer of the plasmid-determined neomycin resistance was of the order of 10^{-5} to 10^{-6} transconjugants per recipient cell (217). Subsequent transfer of neomycin resistance amongst strains of *R. sphaeroides* occurred at a high frequency (about 10^{-2} transconjugants per donor cell). Interestingly, strains of *R. gelatinosa* receiving R68.45 manifest resistance to both neomycin and carbenicillin. In contrast, strains of *R. sphaeroides* acquiring the plasmid are neomycin resistant but remain susceptible to carbenicillin. Transfer of chromosomal markers (notably, antibiotic resistance determinants and restoration of prototrophy to specific auxotrophs) occurred at frequencies of around 10^{-6} to 10^{-7} recombinants per recipient cell for *R. sphaeroides*. Apparently, transfer of R68.45 itself or of chromosomal genes occurs only on solid media (217; cf. reference 84). The preliminary cotransfer data suggest that R68.45 will be a useful genetic tool in the construction of linkage maps of *R. sphaeroides*. Indeed, there is every likelihood that the aforementioned plasmids or relatives will ultimately provide convenient vehicles for manipulating genes within members of the *Rhodospirillaceae*.

The precise mechanism of chromosome mobilization in these cases remains to be elucidated. By analogy with processes of conjugation in *E. coli*, gene transfer may involve some form of covalent association with the chromosome, as in the formation of R-prime plasmids or Hfr donors. Alternatively, the acquired plasmid may direct transfer of chromosomal genes by a mechanism not unlike that postulated for mobilization of non-self-transmissible plasmids and the chromosome by sex factors in *E. coli*. This kind of activity, which is poorly understood, apparently does not involve covalent linkage between plasmid and chromosome (61, 147, 150).

Clearly, a useful objective would be the isolation of stable Hfr donor strains of photosynthetic bacteria for the construction of large-scale genetic maps. The integration of plasmids into the chromosome to form stable Hfr strains is a rare occurrence, the most notable exception being the F factor of *E. coli* (150). However, it may be possible to obtain such strains by exploiting the ability of self-transmissible plasmids to suppress defects in initiation of chromosome replication. This process of integrative suppression (159) has been used in *E. coli* to generate plasmid-mediated Hfr-type strains (147, 151). By constructing mutants of the photosynthetic bacteria which are temperature sensitive for the initiation of DNA replication and by using the capacity of transmissible plasmids to suppress this mutation at the restrictive temperature by insertion into the chromosome, Hfr-type strains may be produced. Moreover, it may be possible to force the selection of Hfr-type strains mediated by IncP plasmids, of which some are already known to be capable of infecting members of the *Rhodospirillaceae*.

CONCLUDING REMARKS

Interest in the genetics of photosynthetic procaryotes has burgeoned considerably over the past decade. The recent advances in genetic manipulation, which now permit transfer and recombination of genetic material within this biological group, justify great expectations for elucidation of the hitherto intransigent genetic systems of these organisms. Indeed, the GTA of *R. capsulata* represents a landmark in the molecular biology of the photosynthetic bacteria. The applicability of the GTA system to fine-structure genetic mapping of *R. capsulata* is clearly demonstrable. However, the limitations of this genetic vector emphasize an urgency for further genetic exchange systems, especially for those capable of transferring longer stretches of the genome and for those capable of establishing stable partial diploids for performance of *cis-trans* complementation analyses. At this time,

transduction and conjugation appear the more promising areas for future developments. The assignment of genetic determinants to plasmids native to photosynthetic procaryotes should facilitate identification of their role, if any, in genetic interplay. Recently, Reanney (186) has expounded the virtues of extrachromosomal elements as executors of evolution in both procaryotes and eucaryotes. He contends that extrachromosomal DNA may have had a dominant rather than peripheral role in the processes of development, adaptation, and speciation. The very presence of plasmids, phage, and the GTA within photosynthetic procaryotes affords scope for such evolutionary mechanisms to have embraced this biological group.

An alternative approach to genetic mapping in the *Rhodospirillaceae*, and one which does not rely directly on any gene transfer system, would be to study the change in mutation frequency of genes at replication. This technique has been successfully used in the construction of temporal genetic maps of the cyanobacterium *A. nidulans* (9, 42, 43, 92). Such temporal genetic maps of *A. nidulans* show good correlation with a conventional genetic map derived from transformation studies (88).

It is conceivable that the sophisticated methodology used in engineering genes within the *Enterobacteriaceae* (see, for example, reference 32) will ultimately be applicable to the photosynthetic bacteria. Genes specifying photopigment production or the ability to fix nitrogen, for instance, could thereby be cloned either within the photosynthetic bacteria themselves or in organisms of more fully defined genetic background, such as *E. coli*. Acquisition of these genes by diverse organisms may facilitate molecular studies on their expression. However, appropriate transformation regimes for the introduction of recombinant DNA into photosynthetic bacteria are wanting at present.

In essence, representatives of the *Rhodospirillaceae* provide attractive experimental systems for the integration of biochemical, biophysical, and genetic technology. Recent trends in the molecular biology of photosynthetic bacteria make it more likely that the full potential of these organisms for ascertaining mechanisms underlying development and function of the photosynthetic apparatus will be realized. A clearer understanding of energy-conserving systems in general should thus ensue.

ACKNOWLEDGMENTS

I thank J. R. Saunders (University of Liverpool, Liverpool, U.K.) for much helpful discussion and constructive criticism of this review, B. L. Marrs (St. Louis University, St. Louis, Mo.), W. R. Sistrom (University of Oregon, Eugene), S. Kaplan (University of Illinois, Urbana), E. W. Frampton (Northern Illinois University, De Kalb), J. D. Wall (Indiana University, Bloomington), and others for making data available prior to publication and for discussion; and T. W. Goodwin (University of Liverpool) for providing research facilities within the Department of Biochemistry during the preparation of this article.

LITERATURE CITED

1. **Abeliovich, A., and S. Kaplan.** 1974. Bacteriophages of *Rhodopseudomonas spheroides*: isolation and characterization of a *Rhodopseudomonas spheroides* bacteriophage. J. Virol. **13**:1392–1399.
2. **Adams, M. H.** 1959. Bacteriophages. Interscience Publishers, Inc., New York.
3. **Adelberg, E. A., M. Mandel, and G. Chein Ching Chen.** 1965. Optimal conditons for mutagenesis by N-methyl-N'-nitro-N-nitrosoguanidine in *Escherichia coli* K 12. Biochem. Biophys. Res. Commun. **18**:788–795.
4. **Adolph, K. W., and R. Haselkorn.** 1972. Photosynthesis and the development of blue-green algal virus N-1. Virology **47**:370–374.
5. **Aitken, A.** 1976. Protein evolution in cyanobacteria. Nature (London) **263**:793–796.
6. **Ambler, R. P.** 1973. Bacterial cytochromes *c* and molecular evolution. Syst. Zool. **22**:554–565.
7. **Ambler, R. P., and R. G. Bartsch.** 1975. Amino acid sequence similarity between cytochrome *f* from a blue-green bacterium and algal chloroplasts. Nature (London) **253**:285–288.
8. **Ambler, R. P., T. E. Meyer, and M. D. Kamen.** 1976. Primary structure determination of two cytochromes *c*: close similarity to functionally unrelated mitochondrial cytochrome *c*. Proc. Natl. Acad. Sci. U.S.A. **73**:472–475.
9. **Asato, Y., and C. E. Folsome.** 1970. Temporal genetic mapping of the blue-green alga, *Anacystis nidulans*. Genetics **65**:407–419.
10. **Asato, Y., and H. S. Ginoza.** 1973. Separation of small circular DNA molecules from the blue-green alga *Anacystis nidulans*. Nature (London) New Biol. **244**:132–133.
11. **Astier, C., and F. Espardellier.** 1976. Mise en évidence d'un système de transfert genétique chez une cyanophycée du genre *Aphanocapsa*. C. R. Acad. Sci. Ser. D. **282**:795–797.
12. **Bachmann, B. J., K. B. Low, and A. L. Taylor.** 1976. Recalibrated linkage map of *Escherichia coli* K-12. Bacteriol. Rev. **40**:116–167.
13. **Barritt, G. J.** 1971. Biosynthesis of isoleucine and valine in *Rhodopseudomonas spheroides*: regulation of threonine deaminase activity. J. Bacteriol. **105**:718–721.
14. **Beremand, P. D., and G. A. Sojka.** 1977. Mutational analysis of serine-glycine biosynthesis in *Rhodopseudomonas capsulata*. J. Bacteriol. **130**:532–534.
15. **Berg, D. E., J. Davies, B. Allet, and J.-D. Rochaix.** 1975. Transposition of R factor genes to bacteriophage λ. Proc. Natl. Acad. Sci. U.S.A. **72**:3628–3632.
16. **Bonen, L., and W. F. Doolittle.** 1975. On the prokaryotic nature of red algal chloroplasts. Proc. Natl. Acad. Sci. U.S.A. **72**:2310–2314.

17. **Bonen, L., and W. F. Doolittle.** 1976. Partial sequences of 16s rRNA and the phylogeny of blue-green algae and chloroplasts. Nature (London) **261**:669–673.
18. **Brock, T. D.** 1973. Evolutionary and ecological aspects of the cyanophytes, p. 487–500. *In* N. G. Carr and B. A. Whitton (ed.), Biology of blue-green algae. Blackwell Scientific Publications, Oxford.
19. **Brown, A. E., F. A. Eiserling, and J. Lascelles.** 1972. Bacteriochlorophyll synthesis and the ultrastructure of wild-type and mutant strains of *Rhodopseudomonas spheroides* Plant Physiol. **50**:743–746.
20. **Bryan, L. E., S. D. Semaka, H. M. Van Den Elzen, J. E. Kinnear, and R. L. S. Whitehouse.** 1973. Characteristics of R931 and other *Pseudomonas aeruginosa* R factors. Antimicrob. Agents Chemother. **3**:625–637.
21. **Buetow, D. E.** 1976. Phylogenetic origin of the chloroplasts. J. Protozool. **23**:41–47.
22. **Burdett, I. D. J., and R. G. E. Murray.** 1974. Electron microscope study of septum formation in *Escherichia coli* strains B and B/r during synchronous growth. J. Bacteriol. **119**:1039–1056.
23. **Carr, N. G., and B. A. Whitton.** 1973. Biology of blue-gree algae. Blackwell Scientific Publications, Oxford.
24. **Chow, C. T.** 1976. Properties of ribonucleic acids from photosynthetic and heterotrophic *Rhodospirillum rubrum*. Can. J. Microbiol. **22**:228–236.
25. **Clark, D. J.** 1968. Regulation of deoxyribonucleic acid replication and cell division in *Escherichia coli* B/r. J. Bacteriol **96**:1214–1224.
26. **Clayton, R. K.** 1963. Photosynthesis: primary physical and chemical processes. Annu. Rev. Plant Physiol. **14**:159–180.
27. **Clayton, R. K.** 1973. Primary processes in bacterial photosynthesis. Annu. Rev. Biophys. Bioeng. **2**:131–156.
28. **Clayton, R. K., and B. J. Clayton.** 1972. Relations between pigments and proteins in the photosynthetic membranes of *Rhodopseudomonas spheroides*. Biochim. Biophys. Acta **283**:492–504.
29. **Clayton, R. K., and C. Smith.** 1960. *Rhodopseudomonas spheroides*: high catalase and blue-green double mutants. Biochem. Biophys. Res. Commun. **3**:143–145.
30. **Cloud, P. E., Jr.** 1965. Significance of the Gunflint Precambrian microflora. Science **148**: 27–35.
31. **Clowes, R. C.** 1972. Molecular structure of bacterial plasmids. Bacteriol. Rev. **36**:361–405.
32. **Cohen, S. N.** 1975. The manipulation of genes. Sci. Am. **233**:24–33.
33. **Cohen, S. N.** 1976. Transposable genetic elements and plasmid evolution. Nature (London) **263**:731–738.
34. **Cohen, S. S.** 1949. Growth requirements of bacterial viruses. Bacteriol. Rev. **13**:1–24.
35. **Cohen, S. S.** 1973. Mitochondria and chloroplasts revisited. Am. Sci. **61**:437–445.
36. **Cohen, Y., B. B. Jørgensen, E. Padan, and M. Shilo.** 1975. Sulphide-dependent anoxygenic photosynthesis in the cyanobacterium *Oscillatoria limnetica*. Nature (London) **257**: 489–492.
37. **Cohen-Bazire, G., W. R. Sistrom, and R. Y. Stanier.** 1957. Kinetic studies of pigment synthesis by non-sulphur purple bacteria. J. Cell. Comp. Physiol. **49**:25–68.
38. **Connelly, J. L., O. T. G. Jones, V. A. Saunders, and D. W. Yates.** 1973. Kinetic and thermodynamic properties of membrane-bound cytochromes of aerobically- and photosynthetically-grown *Rhodopseudomonas spheroides*. Biochim. Biophys. Acta **292**:644–653.
39. **Cuendet, P. A., and H. Zuber.** 1977. Isolation and characterization of a bacteriochlorophyll-associated chromatophore protein from *Rhodospirillum rubrum*–G9. FEBS Lett. **79**: 96–100.
40. **Datta, N., R. W. Hedges, E. J. Shaw, R. B. Sykes, and M. H. Richmond.** 1971. Properties of an R factor from *Pseudomonas aeruginosa*. J. Bacteriol. **108**:1244–1249.
41. **Dayhoff, M. O.** 1976. The origin and evolution of protein superfamilies. Fed. Proc. Fed. Am. Soc. Exp. Biol. **35**:2132–2138.
42. **Delaney, S. F., and N. G. Carr.** 1975. Temporal genetic mapping in the blue-green alga *Anacystis nidulans* using ethyl methane-sulphonate. J. Gen. Microbiol. **88**:259–268.
43. **Delaney, S. F., M. Herdman, and N. G. Carr.** 1976. Genetics of blue-green algae, p. 7–28. *In* R. A. Lewin (ed.), Genetics of the algae. Blackwell Scientific Publications, Oxford.
44. **del Valle-Tascón, S., G. Giménez-Gallego, and J. M. Ramirez.** 1975. Light-dependent ATP formation in a non-phototrophic mutant of *Rhodospirillum rubrum* deficient in oxygen photoreduction. Biochim. Biophys. Res. Commun. **66**:514–519.
45. **del Valle-Tascón, S., G. Giménez-Gallego, and J. M. Ramirez.** 1977. Photooxidase system of *Rhodospirillum rubrum*. I. Photooxidations catalyzed by chromatophores isolated from a mutant deficient in photooxidase activity. Biochim. Biophys. Acta **459**:76–87.
46. **Devilly, C. I., and J. A. Houghton.** 1977. A study of genetic transformation in *Gloeocapsa alpicola*. J. Gen. Microbiol. **98**:277–280.
47. **Dickerson, R. E.** 1972. The structure and history of an ancient protein. Sci. Am. **226**:58–72.
48. **Dickerson, R. E., T. Takano, D. Eisenberg, O. B. Kallai, L. Samson, A. Cooper, and E. Margoliash.** 1971. Ferricytochrome *c*. I. General features of the horse and bonito proteins at 2.8A resolution. J. Biol. Chem. **246**: 1511–1535.
49. **Dickerson, R. E., R. Timkovich, and R. J. Almassy.** 1976. The cytochrome fold and the evolution of bacterial energy metabolism. J. Mol. Biol. **100**:473–491.

50. **Dix, D. E., and C. E. Helmstetter.** 1973. Coupling between chromosome completion and cell division in *Escherichia coli*. J. Bacteriol. **115**:786–795.
51. **Doolittle, W. F.** 1973. Postmaturational cleavage of 23*s* ribosomal ribonucleic acid and its metabolic control in the blue-green alga *Anacystis nidulans*. J. Bacteriol. **113**:1256–1263.
52. **Doolittle, W. F., and L. Bonen.** 1976. Relationships between blue-green algae and chloroplasts revealed by ribosomal RNA sequence characterization, p. 239–241. *In* G. A. Codd and W. D. P. Stewart (ed.), Proceedings of the 2nd International Symposium on Photosynthetic Prokaryotes, Dundee.
53. **Doolittle, W. F., C. R. Woese, M. L. Sogin, L. Bonen, and D. Stahl.** 1975. Sequence studies on 16*s* ribosomal RNA from a blue-green alga. J. Mol. Evol. **4**:307–315.
54. **Drews, G., R. Dierstein, and A. Schumacher.** 1976. Genetic transfer of the capacity to form bacteriochlorophyll-protein complexes in *Rhodopseudomonas capsulata*. FEBS Lett. **68**:132–136.
55. **Drews, G., I. Leutiger, and R. Ladwig.** 1971. Production of protochlorophyll, protopheophytin and bacteriochorophyll by the mutant A1a of *Rhodopseudomonas capsulata*. Arch. Mikrobiol. **76**:349–363.
56. **Dus, K., K. Sletten, and M. D. Kamen.** 1968. Cytochrome c_2 of *Rhodospirillum rubrum*. II. Complete amino acid sequence and phylogenetic relationships. J. Biol. Chem. **243**: 5507–5518.
57. **Dutton, P. L., and J. B. Jackson.** 1972. Thermodynamic and kinetic characterization of electron transfer components *in situ* in *Rhodopseudomonas spheroides* and *Rhodospirillum rubrum*. Eur. J. Biochem. **30**:495–510.
58. **Dutton, P. L., and D. F. Wilson.** 1974. Redox potentiometry in mitochondrial and photosynthetic bioenergetics. Biochim. Biophys. Acta **346**:165–212.
59. **Echlin, P., and I. Morris.** 1965. The relationship between blue-green algae and bacteria. Biol. Rev. Cambridge Philos. Soc. **40**:143–187.
60. **Elsden, S. R.** 1962. Photosynthesis and lithotrophic carbon dioxide fixation, p. 1–40. *In* I. C. Gunsalus and R. Y. Stanier (ed.), The bacteria, vol. 3. Academic Press Inc., London.
61. **Falkow, S.** 1975. Infectious multiple drug resistance. Pion Ltd., London.
62. **Fanica-Gaignier, M., J. Clement-Metral, and M. D. Kamen.** 1971. Adenine nucleotide levels and photopigment synthesis in a growing photosynthetic bacterium. Biochim. Biophys. Acta **226**:135–143.
63. **Fedenko, E. P., E. N. Kondrat'eva, and A. A. Krasnovskii.** 1969. Protochlorophyll mutants of *Rhodopseudomonas palustris*. Nauchn. Dokl. Vyssh. Shk. Biol. Nauki **8**:102–111.
64. **Ferretti, J. F., and E. D. Gray.** 1967. Studies on the adaptive formation of photosynthetic structures in *Rhodopseudomonas spheroides*. II. Nucleotide compositions during adaptation. Biochim. Biophys. Acta **138**:564–569.
65. **Fogg, G. E., W. D. P. Stewart, P. Fay, and A. E. Walsby.** 1973. The blue-green algae. Academic Press Inc., London.
66. **Freund-Mölbert, E., G. Drews, K. Bosecker, and B. Schubel.** 1968. Morphologie und Wirtskreis eines neu isolierten *Rhodopseudomonas palustris* –Phagen. Arch. Mikrobiol. **64**:1–8.
67. **Garcia, A. F., G. Drews, and M. D. Kamen.** 1974. On reconstitution of bacterial photophosphorylation *in vitro*. Proc. Natl. Acad. Sci. U.S.A. **71**:4213–4216.
68. **Garcia, A. F., G. Drews, and M. D. Kamen.** 1975. Electron transport in an *in vitro* reconstituted bacterial photophosphorylating system. Biochim. Biophys. Acta **387**:129–134.
69. **Gest, H.** 1951. Metabolic patterns in photosynthetic bacteria. Bacteriol. Rev. **15**:183–210.
70. **Gest, H.** 1966. Comparative biochemistry of photosynthetic processes. Nature (London) **209**:879–882.
71. **Gest, H.** 1972. Energy conversion and generation of reducing power in bacterial photosynthesis. Adv. Microb. Physiol. **7**:243–282.
72. **Gest, H., M. D. Kamen, and H. M. Bregoff.** 1950. Studies on the metabolism of photosynthetic bacteria. Photoproduction of hydrogen and nitrogen fixation by *Rhodospirillum rubrum*. J. Biol. Chem. **182**:153–170.
73. **Gest, H., A. San Pietro, and L. P. Vernon.** 1963. Bacterial photosynthesis. Antioch Press, Yellow Springs, Ohio.
74. **Gibson, J.** 1968. Control of the photosynthetic apparatus in bacteria, p. 324–331. *In* A. T. Jagendorf and R. C. Fuller (ed.), Comparative biochemistry and biophysics of photosynthesis. University of Tokyo Press, Tokyo.
75. **Gibson, K. D., and R. A. Niederman.** 1970. Characterization of two circular satellite species of deoxyribonucleic acid in *Rhodopseudomonas spheroides*. Arch. Biochem. Biophys. **141**:694–704.
76. **Gottesman, M. M., and J. L. Rosner.** 1975. Acquisition of a determinant for chloramphenicol resistance by coliphage lambda. Proc. Natl. Acad. Sci. U.S.A. **72**:5041–5045.
77. **Gray, E. D.** 1967. Studies on the adaptive formation of photosynthetic structures in *Rhodopseudomonas spheroides*. I. Synthesis of macromolecules. Biochim. Biophys. Acta **138**:550–563.
78. **Gray, E. D.** 1973. Requirement of protein synthesis for maturation of ribosomal RNA in *Rhodopseudomonas spheroides*. Biochim. Biophys. Acta **331**:390–396.
79. **Griffiths, M.** 1962. Further mutational changes in the photosynthetic pigment system of *Rhodopseudomonas spheroides*. J. Gen. Microbiol. **27**:427–435.
80. **Griffiths, M., W. R. Sistrom, G. Cohen-Bazire, and R. Y. Stanier.** 1955. Functions of carotenoids in photosynthesis. Nature (London) **176**:1211–1214.

81. **Griffiths, M., and R. Y. Stanier.** 1956. Some mutational changes in the photosynthetic pigment system of *Rhodopseudomonas spheroides*. J. Gen. Microbiol. **14**:698–715.
82. **Guest, J. R.** 1974. Bacteriocinogeny in the *Athiorhodaceae*. J. Gen. Microbiol. **81**: 513–515.
83. **Guyer, M., and G. Hegeman.** 1969. Evidence for a reductive pathway for the anaerobic metabolism of benzoate. J. Bacteriol. **99**:906–907.
84. **Haas, D., and B. W. Holloway.** 1976. R factor variants with enhanced sex factor activity in *Pseudomonas aeruginosa*. Mol. Gen. Genet. **144**:243–251.
85. **Hardy, K. G.** 1975. Colicinogeny and related phenomena. Bacteriol. Rev. **39**:464–515.
86. **Hedges, R. W., and A. E. Jacob.** 1974. Transposition of ampicillin resistance from RP4 to other replicons. Mol. Gen. Genet. **132**:31–40.
87. **Heffron, F., R. Sublett, R. W. Hedges, A. Jacob, and S. Falkow.** 1975. Origin of the TEM beta-lactamase gene found on plasmids. J. Bacteriol. **122**:250–256.
88. **Herdman, M.** 1973. Transformation in the blue-green alga *Anacystis nidulans* and the associated phenomena of mutation, p. 369–386. *In* L. J. Archer (ed.), Bacterial transformation. Academic Press Inc., London.
89. **Herdman, M.** 1973. Mutations arising during transformation in the blue-green alga *Anacystis nidulans*. Mol. Gen. Genet. **120**:369–378.
90. **Herdman, M.** 1976. The evolution of cyanobacterial genomes, p. 229–231. *In* G. A. Codd and W. D. P. Stewart (ed.), Proceedings of the 2nd International Symposium on Photosynthetic Prokaryotes, Dundee.
91. **Herdman, M., and N. G. Carr.** 1971. Recombination in *Anacystis nidulans* mediated by an extracellular DNA/RNA complex. J. Gen. Microbiol. **68**:xiv–xv.
92. **Herdman, M., B. M. Faulkner, and N. G. Carr.** 1970. Synchronous growth and genome replication in the blue-green alga *Anacystis nidulans*. Arch. Mikrobiol. **73**:238–249.
93. **Hill, L. R.** 1966. An index to deoxyribonucleic acid base compositions of bacterial species. J. Gen. Microbiol. **44**:419–437.
94. **Hong, J. S., and B. N. Ames.** 1971. Localized mutagenesis of any specific small region of the bacterial chromosome. Proc. Natl. Acad. Sci. U.S.A. **68**:3158–3162.
95. **Hsi, E. S. P., and J. R. Bolton.** 1974. Flash photolysis-electron spin resonance study of the effect of *o*-phenanthroline and temperature on the decay time of the ESR signal B1 in reaction center preparations and chromatophores of mutant and wild type strains of *Rhodopseudomonas spheroides* and *Rhodospirillum rubrum*. Biochim. Biophys. Acta **347**:126–133.
96. **Hunter, C. N., and O. T. G. Jones.** 1976. Effect of added light-harvesting pigments on the reconstitution of photosynthetic reactions in membranes from bacteriochlorophyll-less mutants of *Rhodopseudomonas sphaeroides*. Biochem. Soc. Trans. **4**:669–670.
97. **Jacob, F., and E. L. Wollman.** 1959. Lysogeny, p. 319–351. *In* F. M. Burnet and W. M. Stanley (ed.), The viruses, vol. 2. Academic Press Inc., New York.
98. **Jensen, S. L.** 1965. Biosynthesis and function of carotenoid pigments in microorganisms. Annu. Rev. Microbiol. **19**:163–182.
99. **John, P., and F. R. Whatley.** 1975. *Paracoccus denitrificans* and the evolutionary origin of the mitochondrion. Nature (London) **254**:495–498.
100. **Jones, O. T. G.** 1969. Multiple light-induced reactions of cytochromes *b* and *c* in *Rhodopseudomonas spheroides*. Biochem. J. **114**:793–799.
101. **Jones, O. T. G.** 1977. Electron transport and ATP synthesis in the photosynthetic bacteria. Symp. Soc. Gen. Microbiol. **27**:151–183.
102. **Jones, O. T. G., and K. M. Plewis.** 1974. Reconstitution of light-dependent electron transport in membranes from a bacteriochlorophyll-less mutant of *Rhodopseudomonas spheroides*. Biochim. Biophys. Acta **357**:204–215.
103. **Kamen, M. D., and H. Gest.** 1949. Evidence for a nitrogenase system in the photosynthetic bacterium *Rhodospirillum rubrum*. Science **109**:560.
104. **Kaspari, H., and J.-H. Klemme.** 1977. Characterisation of antibiotic activities produced by *Rhodopseudomonas sphaeroides*. FEMS Lett. **1**:59–62.
105. **Keilin, D.** 1966. The history of cell respiration and cytochrome. Cambridge University Press, Cambridge.
106. **Kenyon, C. N., R. Rippka, and R. Y. Stanier.** 1972. Fatty acid composition and physiological properties of some filamentous blue-green algae. Arch. Mikrobiol. **83**:216–236.
107. **Kikuchi, G., and Y. Motokawa.** 1968. Cytochrome oxidase of *Rhodopseudomonas spheroides*, p. 174–181. *In* K. Okunuki, M. D. Kamen, and I. Sezuku (ed.), Structure and function of cytochromes. University Park Press, Baltimore.
108. **Klein, N. C., and L. Mindich.** 1976. Isolation and characterization of a glycerol auxotroph of *Rhodopseudomonas capsulata*: effect of lipid synthesis on the synthesis of photosynthetic pigments. J. Bacteriol. **128**:337–346.
109. **Kondorosi, A., G. B. Kiss, T. Forrai, E. Vincze, and Z. Banfalvi.** 1977. Circular linkage map of *Rhizobium meliloti* chromosome. Nature (London) **268**:525–527.
110. **Kondrat'eva, E. N.** 1965. Photosynthetic bacteria. Israel Program for Scientific Translations, Jerusalem.
111. **Krasnovskii, A. A., E. P. Fedenko, F. Lang, and E. N. Krondrat'eva.** 1970. Spectrofluorimetry of pigments of the parental strain and protochlorophyll mutants of *Rhodopseudomonas palustris*. Dokl. Akad. Nauk SSSR Ser. Biol. **190**:218–221.
112. **Krogmann, D. W.** 1973. Photosynthetic reactions and components of thylakoids, p. 80–98.

In N. G. Carr and B. A. Whitton (ed.), Biology of blue-green algae. Blackwell Scientific Publications, Oxford.

113. **Kuhn, P. J., and S. C. Holt.** 1972. Characterization of a blue mutant of *Rhodospirillum rubrum*. Biochim. Biophys. Acta **261**:267–275.
114. **Kushner, D. J., and C. Breuil.** 1977. Penicillinase (β-lactamase) formation by blue-green algae. Arch. Mikrobiol. **112**:219–223.
115. **La Monica, R. F., and B. L. Marrs.** 1976. The branched respiratory system of photosynthetically-grown *Rhodopseudomonas capsulata*. Biochim. Biophys. Acta **423**:431–439.
116. **Lascelles, J.** 1966. The accumulation of bacteriochlorophyll precursors by mutant and wild type strains of *Rhodopseudomonas spheroides*. Biochem. J. **100**:175–183.
117. **Lascelles, J.** 1966. The regulation of synthesis of iron and magnesium tetrapyrroles. Observations with mutant strains of *Rhodopseudomonas spheroides*. Biochem. J. **100**:184–189.
118. **Lascelles, J.** 1968. The bacterial photosynthetic apparatus. Adv. Microb. Physiol. **2**:1–42.
119. **Lascelles, J.** 1975. The regulation of heme and chlorophyll synthesis in bacteria. Ann. N.Y. Acad. Sci. **244**:334–347.
120. **Lascelles, J., and T. Altshuler.** 1967. Some properties of mutant strains of *Rhodopseudomonas spheroides* which do not form bacteriochlorophyll. Arch. Mikrobiol. **59**:204–210.
121. **Lascelles, J., and T. Altshuler.** 1969. Mutant strains of *Rhodopseudomonas spheroides* lacking δ-aminolevulinate synthase: growth, heme, and bacteriochlorophyll synthesis. J. Bacteriol. **98**:721–727.
122. **Lascelles, J., and T. P. Hatch.** 1969. Bacteriochlorophyll and heme synthesis in *Rhodopseudomonas spheroides*: possible role of heme in regulation of the branched biosynthetic pathway. J. Bacteriol. **98**:712–720.
123. **Lascelles, J., and D. Wertlieb.** 1971. Mutant strains of *Rhodopseudomonas spheroides* which form photosynthetic pigments aerobically in the dark. Biochim. Biophys. Acta **226**:328–340.
124. **Lederberg, J.** 1950. Isolation and characterization of biochemical mutants in bacteria. Methods Med. Res. **3**:5–22.
125. **Lessie, T. G.** 1965. The atypical ribosomal RNA complement of *Rhodopseudomonas spheroides*. J. Gen. Microbiol. **39**:311–320.
126. **Lessie, T. G., and W. R. Sistrom.** 1964. Control of porphyrin synthesis in *Rhodopseudomonas spheroides*. Biochim. Biophys. Acta **86**: 250–259.
127. **Lewin, R. A.** 1976. Prochlorophyta as a proposed new division of algae. Nature (London) **261**:697–698.
128. **Lien, S., H. Gest, and A. San Pietro.** 1973. Regulation of chlorophyll synthesis in photosynthetic bacteria. Bioenergetics **4**:423–434.
129. **Lien, S., A. San Pietro, and H. Gest.** 1971. Mutational and physiological enhancement of photosynthetic energy conversion in *Rhodopseudomonas capsulata*. Proc. Natl. Acad. Sci. U.S.A. **68**:1912–1915.
130. **Linton, A. H.** 1977. Antibiotic resistance: the present situation reviewed. Vet. Rec. **100**: 354–360.
131. **Lueking, D., L. Pike, and G. Sojka.** 1976. Glycerol utilization by a mutant of *Rhodopseudomonas capsulata*. J. Bacteriol. **125**:750–752.
132. **Lueking, D., D. Tokuhisa, and G. Sojka.** 1973. Glycerol assimilation by a mutant of *Rhodopseudomonas capsulata*. J. Bacteriol. **115**: 897–903.
133. **Mandel, M., E. R. Leadbetter, N. Pfennig, and H. G. Trüper.** 1971. Deoxyribonucleic acid base compositions of phototrophic bacteria. Int. J. Syst. Bacteriol. **21**:222–230.
134. **Mann, N., and N. G. Carr.** 1974. Control of macromolecular composition and cell division in the blue-green alga *Anacystis nidulans*. J. Gen. Microbiol. **83**:399–405.
135. **Mann, N., and N. G. Carr.** 1977. Coupling between initiation of DNA replication and cell division in the blue-green alga *Anacystis nidulans*. Arch. Mikrobiol. **112**:95–98.
136. **Margulis, L.** 1970. Origin of eukaryotic cells. Yale University Press, New Haven, Conn.
137. **Marrs, B.** 1976. The resolution of two contributing mutations in blue-green mutants of *Rhodopseudomonas capsulata*, p. 227. *In* G. A. Codd and W. D. P. Stewart (ed.), Proceedings of the 2nd International Symposium on Photosynthetic Prokaryotes, Dundee.
138. **Marrs, B., and H. Gest.** 1973. Genetic mutations affecting the respiratory electron-transport system of the photosynthetic bacterium *Rhodopseudomonas capsulata*. J. Bacteriol. **114**:1045–1051.
139. **Marrs, B., and H. Gest.** 1973. Regulation of bacteriochlorophyll synthesis by oxygen in respiratory mutants of *Rhodopseudomonas capsulata*. J. Bacteriol. **114**:1052–1057.
140. **Marrs, B., and S. Kaplan.** 1970. 23*s* precursor ribosomal RNA of *Rhodopseudomonas spheroides*. J. Mol. Biol. **49**:297–317.
141. **Marrs, B., C. L. Stahl, S. Lien, and H. Gest.** 1972. Biochemical physiology of respiration-deficient mutant of the photosynthetic bacterium *Rhodopseudomonas capsulata*. Proc. Natl. Acad. Sci. U.S.A. **64**:916–920.
142. **Marrs, B. L.** 1974. Genetic recombination in *Rhodopseudomonas capsulata*. Proc. Natl. Acad. Sci. U.S.A. **71**:971–973.
143. **Marrs, B. L.** 1977. Genetics and bacteriophage. *In* R. K. Clayton and W. R. Sistrom (ed.), The photosynthetic bacteria. Plenum Publishing Corp., New York.
144. **Marvin, D. A., and B. Hohn.** 1969. Filamentous bacterial viruses. Bacteriol. Rev. **33**:172–209.
145. **Maudinas, B., H. Rolin, M. Pierfitte, and J. Villoutreix.** 1972. Etudes des caroténoides de mutants de *Rhodopseudomonas spheroides* C. R. Soc. Biol. **166**:1091–1094.
146. **Mereschkowsky, C.** 1905. Über Natur und Ursprung der Chromatophoren in Pflanzenreiche.

Biol. Zentralbl. **25**:593–604.
147. **Meynell, G. G.** 1972. Bacterial plasmids. The Macmillan Press Ltd., London.
148. **Mitronova, T. N., S. V. Shestakov, and V. D. Zhevner.** 1973. Properties of a radiosensitive filamentous mutant of the blue-green alga *Anacystis nidulans*. Mikrobiologiya **42**:519–524.
149. **Møller, J. K., A. L. Bak, C. Christiansen, G. Christiansen, and A. Stenderup.** 1976. Extrachromosomal deoxyribonucleic acid in R factor-harboring *Enterobacteriaceae*. J. Bacteriol. **125**:398–403.
150. **Moody, E. E. M., and W. Hayes.** 1972. Chromosome transfer by autonomous transmissible plasmids: the role of the bacterial recombination (*rec*) system. J. Bacteriol. **111**:80–85.
151. **Moody, E. E. M., and R. Runge.** 1972. The integration of autonomous transmissible plasmids into the chromosome of *Escherichia coli* K12. Genet. Res. **19**:181–186.
152. **Moore, R. L., and B. J. McCarthy.** 1969. Characterization of the deoxyribonucleic acid of various strains of halophilic bacteria. J. Bacteriol. **99**:248–254.
153. **Mural, R. J., and D. I. Friedman.** 1974. Isolation and characterization of a temperate bacteriophage specific for *Rhodopseudomonas spheroides*. J. Virol. **14**:1288–1292.
154. **Nevers, P., and H. Saedler.** 1977. Transposable genetic elements as agents of gene instability and chromosomal rearrangements. Nature (London) **268**:109–115.
155. **Newton, J. W.** 1967. Bacilliform mutants of *Rhodospirillum rubrum*. Biochim. Biophys. Acta **141**:633–636.
156. **Newton, J. W.** 1968. Linkages in the walls of *Rhodospirillum rubrum* and its bacilliform mutants. Biochim. Biophys. Acta **165**:534–537.
157. **Newton, J. W.** 1970. Metabolism of D-alanine in *Rhodospirillum rubrum* and its bacilliform mutants. Nature (London) **228**:1100–1101.
158. **Newton, J. W.** 1971. Vibrio mutants of *Rhodospirillum rubrum*. Biochim. Biophys. Acta **244**:478–480.
159. **Nishimura, Y., L. Caro, C. M. Berg, and Y. Hirota.** 1971. Chromosome replication in *Escherichia coli*. IV. Control of chromosome replication and cell division by an integrated episome. J. Mol. Biol. **55**:441–456.
160. **Novick, R. P.** 1969. Extrachromosomal inheritance in bacteria. Bacteriol. Rev. **33**:210–263.
161. **Novick, R. P.** 1974. Bacterial plasmids, p. 537–586. *In* A. I. Laskin and H. A. Lechevalier (ed.), Handbook of microbiology, vol. 4, Microbial metabolism, genetics and immunology. CRC Press, Cleveland.
162. **Novick, R. P., R. C. Clowes, S. N. Cohen, R. Curtiss III, N. Datta, and S. Falkow.** 1976. Uniform nomenclature for bacterial plasmids: a proposal. Bacteriol. Rev. **40**:168–189.
163. **Oelze, J., and G. Drews.** 1970. The production of particle bound bacteriochlorophyll precursors by the mutant F9 of *Rhodospirillum rubrum*. Arch. Mikrobiol. **73**:19–33.
164. **Oelze, J., and G. Drews.** 1972. Membranes of photosynthetic bacteria. Biochim. Biophys. Acta **265**:209–239.
165. **Oelze, J., J. Schroeder, and G. Drews.** 1970. Bacteriochlorophyll, fatty-acid, and protein synthesis in relation to thylakoid formation in mutant strains of *Rhodospirillum rubrum*. J. Bacteriol. **101**:669–674.
166. **Oishi, M., and R. M. Irbe.** 1977. Circular chromosomes and genetic transformation in *Escherichia coli*, p. 121–134. *In* A. Portolés, R. López, and M. Espinosa (ed.), Modern trends in bacterial transformation and transfection. Elsevier Biomedical Press, Amsterdam.
167. **Olsen, R. H., and P. Shipley.** 1973. Host range and properties of the *Pseudomonas aeruginosa* R factor R1822. J. Bacteriol. **113**: 772–780.
168. **Olson, J. M.** 1970. The evolution of photosynthesis. Science **168**:438–446.
169. **Orkwiszewski, K. G., and A. R. Kaney.** 1974. Genetic transformation of the blue-green bacterium *Anacystis nidulans*. Arch. Mikrobiol. **98**:31–37.
170. **Ormerod, J. G., and H. Gest.** 1962. Symposium on metabolism of inorganic compounds. IV. Hydrogen photosynthesis and alternative metabolic pathways in photosynthetic bacteria. Bacteriol. Rev. **26**:51–66.
171. **Padan, E., D. Ginzburg, and M. Shilo.** 1970. The reproductive cycle of cyanophage LPP1-G in *Plectonema boryanum* and its dependence on photosynthetic and respiratory systems. Virology **40**:514–521.
172. **Padan, E., and M. Shilo.** 1973. Cyanophages—viruses attacking blue-green algae. Bacteriol. Rev. **37**:343–370.
173. **Parson, W. W.** 1974. Bacterial photosynthesis. Annu. Rev. Microbiol. **28**:41–59.
174. **Parson, W. W., and R. J. Cogdell.** 1975. The primary photochemical reaction of bacterial photosynthesis. Biochim. Biophys. Acta **416**:105–149.
175. **Payne, P. I., and T. A. Dyer.** 1972. Characterization of ribosomal ribonucleic acids of blue-green algae. Arch. Mikrobiol. **87**:29–40.
176. **Pemberton, J. M., and W. T. Tucker.** 1977. Naturally occurring viral R plasmid with a circular supercoiled genome in the extracellular state. Nature (London) **266**:50–51.
177. **Pfennig, N.** 1967. Photosynthetic bacteria. Annu. Rev. Microbiol. **21**:285–324.
178. **Pfennig, N.** 1970. Dark growth of phototrophic bacteria under microaerophilic conditions. J. Gen. Microbiol. **61**:ii–iii.
179. **Pfennig, N.** 1977. Phototrophic green and purple bacteria: a comparative systematic survey. Annu. Rev. Microbiol. **31**:275–290.
180. **Pfennig, N., and H. G. Trüper.** 1974. The phototrophic bacteria, p. 24–75. *In* R. E. Buchanan and N. E. Gibbons (ed.), Bergey's manual of determinative bacteriology, 8th ed. The Williams & Wilkins Co., Baltimore.
181. **Picorel, R., S. del Valle-Tascón, and J. M. Ramirez.** 1977. Isolation of a photosynthetic strain of *Rhodospirillum rubrum* with an al-

tered reaction center. Arch. Biochem. Biophys. **181**:665–670.
182. **Pike, L., and G. A. Sojka.** 1975. Glycerol dissimilation in *Rhodopseudomonas sphaeroides*. J. Bacteriol. **124**:1101–1105.
183. **Pradel, J., and J. D. Clement-Metral.** 1976. A 4-vinyl protochlorophyllide complex accumulated by "Phofil" mutant of *Rhodopseudomonas spheroides*. An authentic intermediate in the development of the photosynthetic apparatus. Biochim. Biophys. Acta **430**:253–264.
184. **Pudek, M. R., and W. R. Richards.** 1975. A possible alternate pathway of bacteriochlorophyll biosynthesis in a mutant of *Rhodopseudomonas sphaeroides*. Biochemistry **14**: 3132–3137.
185. **Raven, P. H.** 1970. A multiple origin for plastids and mitochondria. Science **169**:641–646.
186. **Reanney, D.** 1976. Extrachromosomal elements as possible agents of adaptation and development. Bacteriol. Rev. **40**:552–590.
187. **Restaino, L., and E. W. Frampton.** 1975. Labeling the deoxyribonucleic acid of *Anacystis nidulans*. J. Bacteriol. **124**:155–160.
188. **Richards, W. R., and J. Lascelles.** 1969. The biosynthesis of bacteriochlorophyll. The characterization of latter stage intermediates from mutants of *Rhodopseudomonas spheroides* Biochemistry **8**:3473–3482.
189. **Richmond, M. H.** 1973. Resistance factors and their ecological importance to bacteria and to man. Prog. Nucleic Acid Res. Mol. Biol. **13**:191–248.
190. **Richmond, M. H., and R. B. Sykes.** 1973. The β-lactamases of gram-negative bacteria and their possible physiological role. Adv. Microb. Physiol. **9**:31–88.
191. **Rimon, A., and A. B. Oppenheim.** 1974. Isolation and genetic mapping of temperature-sensitive mutants of cyanophage LPP2-SP1. Virology **62**:567–569.
192. **Roberts, T. M., L. C. Klotz, and A. R. Loeblich III.** 1977. Characterization of a blue-green algal genome. J. Mol. Biol. **110**:341–361.
193. **Roberts, T. M., and K. E. Koths.** 1976. The blue-green alga *Agmenellum quadruplicatum* contains covalently closed DNA circles. Cell **9**:551–557.
194. **Robinson, A., and J. Sykes.** 1971. A study of the atypical ribosomal RNA components of *Rhodopseudomonas spheroides*. Biochim. Biophys. Acta **238**:99–115.
195. **Safferman, R. S.** 1973. Phycoviruses, p. 214–237. *In* N. G. Carr and B. A. Whitton (ed.), Biology of blue-green algae. Blackwell Scientific Publications, Oxford.
196. **Safferman, R. S., and M. E. Morris.** 1963. Algal virus: isolation. Science **140**:679–680.
197. **Sagan, L.** 1967. On the origin of mitosing cells. J. Theor. Biol. **14**:225–274.
198. **Salemme, F. R., S. T. Freer, Ng. H. Xuong, R. A. Alden, and J. Kraut.** 1973. The structure of oxidized cytochrome c_2 of *Rhodospirillum rubrum*. J. Biol. Chem. **248**:3910–3921.
199. **Sanderson, K. E.** 1972. Linkage map of *Salmonella typhimurium*, edition IV. Bacteriol. Rev. **36**:558–586.
200. **Saunders, J. R.** 1975. Transposable resistance genes. Nature (London) **258**:384.
201. **Saunders, J. R.** 1976. Plasmid exclusion and incompatibility. Nature (London) **260**: 665–666.
202. **Saunders, J. R., and R. B. Sykes.** 1977. Transfer of a plasmid-specified beta-lactamase gene from *Haemophilus influenzae*. Antimicrob. Agents Chemother. **11**:339–344.
203. **Saunders, V. A., and O. T. G. Jones.** 1974. Adaptation in *Rhodopseudomonas spheroides*. FEBS Lett. **44**:169–172.
204. **Saunders, V. A., and O. T. G. Jones.** 1974. Properties of the cytochrome *a*-like material developed in the photosynthetic bacterium *Rhodopseudomonas spheroides* when grown aerobically. Biochim. Biophys. Acta **333**: 439–445.
205. **Saunders, V. A., and O. T. G. Jones.** 1975. Detection of two further *b*-type cytochromes in *Rhodopseudomonas spheroides*. Biochim. Biophys. Acta **396**:220–228.
206. **Saunders, V. A., J. R. Saunders, and P. M. Bennett.** 1976. Extrachromosomal deoxyribonucleic acid in wild-type and photosynthetically incompetent strains of *Rhodopseudomonas spheroides*. J. Bacteriol. **125**:1180–1187.
207. **Schick, J., and G. Drews.** 1969. The morphogenesis of the bacterial photosynthetic apparatus. III. The features of a pheophytin-protein-carbohydrate complex excreted by the mutant M46 of *Rhodospirillum rubrum*. Biochim. Biophys. Acta **183**:215–229.
208. **Schmidt, L. S., H.-C. Yen, and H. Gest.** 1974. Bioenergetic aspects of bacteriophage replication in the photosynthetic bacterium *Rhodopseudomonas capsulata*. Arch. Biochem. Biophys. **165**:229–239.
209. **Schön, G.** 1969. The influence of cultural conditions on the ATP-, ADP- and AMP- pool of *Rhodospirillum rubrum*. Arch. Mikrobiol. **66**:348–364.
210. **Segen, B. J., and K. D. Gibson.** 1971. Deficiencies of chromatophore proteins in some mutants of *Rhodopseudomonas spheroides* with altered carotenoids. J. Bacteriol. **105**:701–709.
211. **Sherman, L. A., and R. K. Clayton.** 1972. Lack of carotenoid band shifts in a non-photosynthetic reaction centerless mutant of *Rhodopseudomonas spheroides*. FEBS Lett. **22**: 127–132.
212. **Sherman, L. A., and M. Connelly.** 1976. Isolation and characterization of a cyanophage infecting the unicellular blue-green alga *A. nidulans* and *S. cedrorum*. Virology **72**:540–544.
213. **Shestakov, S. V., and N. T. Khyen.** 1970. Evidence for genetic transformation in blue-green alga *Anacystis nidulans*. Mol. Gen. Genet. **107**:372–375.
214. **Shin, M., M. Sukenobu, R. Oshino, and Y. Kitazume.** 1977. Two plant-type ferredoxins from the blue-green alga *Nostoc verrucosum*. Biochim. Bioophys. Acta **460**:85–93.

215. **Silver, M., S. Friedman, R. Guay, J. Couture, and R. Tanguay.** 1971. Base composition of deoxyribonucleic acid isolated from *Athiorhodaceae*. J. Bacteriol. **107**:368–370.
216. **Sistrom, W. R.** 1966. The spectrum of bacteriochlorophyll *in vivo*: observations on mutants of *Rhodopseudomonas spheroides*. Photochem. Photobiol. **5**:845–856.
217. **Sistrom, W. R.** 1977. Transfer of chromosomal genes mediated by plasmid R68.45 in *Rhodopseudomonas sphaeroides*. J. Bacteriol. **131**:526–532.
218. **Sistrom, W. R., and R. K. Clayton.** 1964. Studies on a mutant of *Rhodopseudomonas spheroides* unable to grow photosynthetically. Biochim. Biophys. Acta **88**:61–73.
219. **Sistrom, W. R., M. Griffiths, and R. Y. Stanier.** 1956. The biology of a photosynthetic bacterium which lacks coloured carotenoids. J. Cell. Comp. Physiol. **48**:473–515.
220. **Sistrom, W. R., B. M. Ohlsson, and J. Crounce.** 1963. Absence of light-induced absorbancy changes in a mutant of *Rhodopseudomonas spheroides* unable to grow photosynthetically. Biochim. Biophys. Acta **75**: 285–286.
221. **Solioz, M., and B. Marrs.** 1977. The gene transfer agent of *Rhodopseudomonas capsulata*. Purification and characterization of its nucleic acid. Arch. Biochem. Biophys. **181**:300–307.
222. **Solioz, M., H.-C. Yen, and B. Marrs.** 1975. Release and uptake of gene transfer agent by *Rhodopseudomonas capsulata*. J. Bacteriol. **123**:651–657.
223. **Solov'eva, Zh. V., and E. P. Fedenko.** 1970. Ultrafine cell structure of the parent strain and the pigmented mutant of *Rhodopseudomonas palustris*. Microbiology (USSR) **39**:94–97.
224. **Stanier, R. Y.** 1961. Photosynthetic mechanisms in bacteria and plants: development of a unitary concept. Bacteriol. Rev. **25**:1–17.
225. **Stanier, R. Y.** 1970. Some aspects of the biology of cells and their possible evolutionary significance. Symp. Soc. Gen. Microbiol. **20**:1–38.
226. **Stanier, R. Y.** 1974. The origins of photosynthesis in eukaryotes. Symp. Soc. Gen. Microbiol. **24**:219–240.
227. **Stanier, R. Y., R. Kunisawa, M. Mandel, and G. Cohen-Bazire.** 1971. Purification and properties of unicellular blue-green algae (order *Chroococcales*). Bacteriol. Rev. **35**:171–205.
228. **Stanier, R. Y., and J. H. C. Smith.** 1959. Protochlorophyll from a purple bacterium. Carnegie Inst. Washington Yearb. **58**:336–338.
229. **Stanier, R. Y., and C. B. van Niel.** 1962. The concept of a bacterium. Arch. Mikrobiol. **42**:17–35.
230. **Starlinger, P., and H. Saedler.** 1972. Insertion mutations in microorganisms. Biochimie **54**:177–185.
231. **Stent, G. S.** 1963. Molecular biology of bacterial viruses. W. H. Freeman & Co., San Francisco.
232. **Stewart, W. D. P.** 1973. Nitrogen fixation by photosynthetic microorganisms. Annu. Rev. Microbiol. **27**:283–316.
233. **Stewart, W. D. P.** 1973. Nitrogen fixation, p. 260–278. *In* N. G. Carr and B. A. Whitton (ed.), Biology of blue-green algae. Blackwell Scientific Publications, Oxford.
234. **Stewart, W. D. P.** 1975. Nitrogen fixation by free-living microorganisms. Cambridge University Press, Cambridge.
235. **Suyama, Y., and J. Gibson.** 1966. Satellite DNA in photosynthetic bacteria. Biochem. Biophys. Res. Commun. **24**:549–553.
236. **Sybesma, C.** 1969. Light-induced reactions of P890 and P800 in the purple photosynthetic bacterium *Rhodospirillum rubrum*. Biochim. Biophys. Acta **172**:177–179.
237. **Tabita, F. R., S. E. Stevens, Jr., and R. Quijano.** 1974. D-ribulose 1,5-diphosphate carboxylase from blue-green algae. Biochem. Biophys. Res. Commun. **61**:45–52.
238. **Takemoto, J., and J. Lascelles.** 1973. Coupling between bacteriochlorophyll and membrane protein synthesis in *Rhodopseudomonas spheroides*. Proc. Natl. Acad. Sci. U.S.A. **70**:799–803.
239. **Takemoto, J., and J. Lascelles.** 1974. Function of membrane proteins coupled to bacteriochlorophyll synthesis. Arch. Biochem. Biophys. **163**:507–514.
240. **Tanaka, M., M. Haniu, K. T. Yasunobu, M. C. W. Evans, and K. K. Rao.** 1974. Amino acid sequence of ferredoxin from a photosynthetic green bacterium, *Chlorobium limicola*. Biochemistry **13**:2953–2959.
241. **Tanaka, M., M. Haniu, K. T. Yasunobu, M. C. W. Evans, and K. K. Rao.** 1975. The amino acid sequence of ferredoxin II from *Chlorobium limicola*, a photosynthetic green bacterium. Biochemistry **14**:1938–1943.
242. **Tanaka, M., M. Haniu, K. T. Yasunobu, K. K. Rao, and D. O. Hall.** 1975. Modification of the automated sequence determination as applied to the sequence determination of the *Spirulina maxima* ferredoxin. Biochemistry **14**:5535–5540.
243. **Taylor, A. L., and C. D. Trotter.** 1972. Linkage map of *Escherichia coli* strain K-12. Bacteriol. Rev. **36**:504–524.
244. **Taylor, F. J. R.** 1974. Implications and extensions of the serial endosymbiosis theory of the origin of eukaryotes. Taxon **23**:229–258.
245. **Tedro, S. M., T. E. Meyer, and M. D. Kamen.** 1976. Primary structure of a high potential iron-sulfur protein from the purple non-sulfur photosynthetic bacterium *Rhodopseudomonas gelatinosa*. J. Biol. Chem. **251**:129–136.
246. **Thorne, C. B.** 1974. Transduction, p. 517–521. *In* A. I. Laskin and H. A. Lechevalier (ed.), Handbook of microbiology, vol. 4, Microbial metabolism, genetics and immunology. CRC Press, Cleveland, Ohio.
247. **Timkovich, R., and R. E. Dickerson.** 1973. Recurrence of the cytochrome fold in a nitrate-respiring bacterium. J. Mol. Biol. **79**:39–56.
248. **Timkovich, R., and R. E. Dickerson.** 1976. The structure of *Paracoccus denitrificans* cytochrome c_{550}. J. Biol. Chem. **251**:4033–4046.

249. **Timkovich, R., R. E. Dickerson, and E. Margoliash.** 1976. Amino acid sequence of *Paracoccus denitrificans* cytochrome c_{550} J. Biol. Chem. **251**:2197-2206.
250. **Uffen, R. L., C. Sybesma, and R. S. Wolfe.** 1971. Mutants of *Rhodospirillum rubrum* obtained after long-term anaerobic, dark growth. J. Bacteriol. **108**:1348-1356.
251. **Uffen, R. L., and R. S. Wolfe.** 1970. Anaerobic growth of purple nonsulfur bacteria under dark conditions. J. Bacteriol. **104**:462-472.
252. **Uspenskaya, V. É., and G. V. Lyskova.** 1972. Synthesis of pigments by a mutant of *Rhodopseudomonas* under different conditions of growth. Microbiology (USSR) **41**:919-924.
253. **Utkilen, H. C.** 1976. Thiosulphate as electron donor in the blue-green alga *Anacystis nidulans*. J. Gen. Microbiol. **95**:177-180.
254. **Van Baalen, C.** 1973. Mutagenesis and genetic recombination, p. 201-213. *In* N. G. Carr and B. A. Whitton (ed.), Biology of blue-green algae. Blackwell Scientific Publications, Oxford
255. **Van Beeumen, J., R. P. Ambler, T. E. Meyer, M. D. Kamen, J. M. Olson, and E. K. Shaw.** 1976. The amino acid sequences of the cytochromes *c*555 from two green sulphur bacteria of the genus *Chlorobium*. Biochem. J. **159**:757-774.
256. **Van Grondelle, R., L. N. M. Duysens, and H. N. Van der Wal.** 1976. Function of three cytochromes in photosynthesis of whole cells of *Rhodospirillum rubrum* as studied by flash spectroscopy. Evidence for two types of reaction center. Biochim. Biophys. Acta **449**: 169-187.
257. **van Niel, C. B.** 1944. The culture, general physiology, morphology, and classification of the non-sulfur and brown bacteria. Bacteriol. Rev. **8**:1-118.
258. **Van Niel, C. B.** 1954. The chemoautotrophic and photosynthetic bacteria. Annu. Rev. Microbiol. **8**:105-132.
259. **Vernon, L. P.** 1964. Bacterial photosynthesis. Plant Physiol. **15**:73-100.
260. **Wada, K., T. Hase, H. Tokunaga, and H. Matsubara.** 1975. Amino acid sequence of *Spirulina platensis* ferredoxin: a far divergency of blue-green algal ferredoxins. FEBS Lett. **55**:102-104.
261. **Wall, J. D., and H. Gest.** 1974. Prospects for the molecular biology of photosynthetic bacteria. Proc. Int. Congr. Photosynth. Res. **3**:1179-1188.
262. **Wall, J. D., B. C. Johansson, and H. Gest.** 1976. Nif$^-$ mutants of *Rhodopseudomonas capsulata*, p. 234-235. *In* G. A. Codd and W. D. P. Stewart (ed.), Proceedings of the 2nd International Symposium on Photosynthetic Prokaryotes, Dundee.
263. **Wall, J. D., P. F. Weaver, and H. Gest.** 1975. Gene transfer agents, bacteriophage and bacteriocins of *Rhodopseudomonas capsulata*. Arch. Mikrobiol. **105**:217-224.
264. **Wall, J. D., P. F. Weaver, and H. Gest.** 1975. Genetic transfer of nitrogenase-hydrogenase activity in *Rhodopseudomonas capsulata*. Nature (London) **258**:630-631.
265. **Watson, J. D.** 1975. Molecular biology of the gene. W. A. Benjamin Inc., London.
266. **Weaver, P.** 1971. Temperature sensitive mutants of the photosynthetic apparatus of *Rhodospirillum rubrum*. Proc. Natl. Acad. Sci. U.S.A. **68**:136-138.
267. **Weaver, P. F., J. D. Wall, and H. Gest.** 1975. Characterization of *Rhodopseudomonas capsulata*. Arch. Mikrobiol. **105**:207-216.
268. **Westmacott, D., and S. B. Primrose.** 1977. The effect of nalidixic acid on the cell cycle of synchronous *Rhodopseudomonas palustris* cultures. J. Gen. Microbiol. **98**:155-166.
269. **Willetts, N. S.** 1972. The genetics of transmissible plasmids. Annu. Rev. Genet. **6**:257-268.
270. **Witkin, S. S., and K. D. Gibson.** 1972. Changes in ribonucleic acid turnover during aerobic and anaerobic growth in *Rhodopseudomonas spheroides*. J. Bacteriol. **110**:677-683.
271. **Witkin, S. S., and K. D. Gibson.** 1972. Ribonucleic acid from aerobically and anaerobically grown *Rhodopseudomonas spheroides*: comparison by hybridization to chromosomal and satellite deoxyribonucleic acid. J. Bacteriol. **110**:684-690.
272. **Wittenberg, T., and W. R. Sistrom.** 1971. Mutant of *Rhodopseudomonas spheroides* unable to grow aerobically. J. Bacteriol. **106**:732-738.
273. **Wolk, C. P.** 1973. Physiology and cytological chemistry of blue-green algae. Bacteriol. Rev. **37**:32-101.
274. **Yamashita, J., and M. D. Kamen.** 1968. Observations on the nature of pulse-labelled RNA's from photosynthetically or heterotrophically-grown *Rhodospirillum rubrum*. Biochim. Biophys. Acta **161**:162-169.
275. **Yasunobu, K. T., and M. Tanaka.** 1973. The evolution of iron-sulfur protein containing organisms. Syst. Zool. **22**:570-589.
276. **Yen, H.-C., and B. Marrs.** 1976. Map of genes for carotenoid and bacteriochlorophyll biosynthesis in *Rhodopseudomonas capsulata*. J. Bacteriol. **126**:619-629.
277. **Yen, H.-C., and B. Marrs.** 1977. Growth of *Rhodopseudomonas capsulata* under anaerobic dark conditions with dimethyl sulfoxide. Arch. Biochem. Biophys. **181**:411-418.
278. **Zannoni, D., A. Baccarini-Melandri, B. A. Melandri, E. H. Evans, R. C. Prince, and A. R. Crofts.** 1974. Energy transduction in photosynthetic bacteria: the nature of cytochrome *c* oxidase in the respiratory chain of *Rhodopseudomonas capsulata*. FEBS Lett. **48**: 152-155.
279. **Zannoni, D., B. A. Melandri, and A. Baccarini-Melandri.** 1976. Energy transduction in photosynthetic bacteria. X. Composition and function of the branched oxidase system in wild type and respiration deficient mutants of *Rhodopseudomonas capsulata*. Biochim. Biophys. Acta **423**:413-430.
280. **Zannoni, D., B. A. Melandri, and A. Baccarini-Melandri.** 1976. Energy transduction in

photosynthetic bacteria. XI. Further resolution of cytochromes of *b*-type and the nature of the CO-sensitive oxidase present in the respiratory chain of *Rhodopseudomonas capsulata*. Biochim. Biophys. Acta **449**:386–400.

281. **Zilinsky, J. W., G. A. Sojka, and H. Gest.** 1971. Energy charge regulation in photosynthetic bacteria. Biochem. Biophys. Res. Commun. **42**:955–961.